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SHELL SEXUAL DIMORPHISM OF *MARGARITES VORTICIFERA*: MULTIVARIANT ANALYSIS AND TAXONOMIC IMPLICATIONS

David R. Lindberg[1]

ABSTRACT

A discriminant function analysis was performed on a data set from the shells of the sexually dimorphic trochid gastropod *Margarites vorticifera*. The data set consisted of four shell parameters (position of generating curve, whorl translation, whorl expansion rate and apertural shape) for each male and female snail. Shell parameters from the type specimens of the four synonyms of this species also were analyzed and their probable sex determined. Shell sexual dimorphism in *M. vorticifera* is primarily a result of changes in the position of the generating curve in relation to the shell axis and to a lesser extent due to changes in the whorl expansion rate; these same characters have been used to distinguish some of the nominal species. Neontological and paleontological applications of discriminant function analysis include identification of morphological differences, identification of statistically typical specimens, and the association of biochemical and/or anatomical characters with hard-part morphology.

INTRODUCTION

Sexual dimorphism of gastropod shells can occur as either size differences or shape differences. Size differences are more common and have been reported in many taxa (for reviews, see Lamy, 1937; Sohl, 1969; Carlton, 1977; Webber, 1977). Shape differences include ornamentation (Amio, 1955; Sohl, 1960; Abbott, 1968), apertural shape (Robertson, 1971; Demian & Ibrahim, 1972), and differences in the rate of expansion of the generating curve of the shell (Linsley, 1978). As pointed out by Linsley (1978: 33), shape differences may "be adaptive to accommodate the bulky eggs produced by the female."

While many of the properties of sexual dimorphism in shell shape of gastropods are of interest to reproductive biologists, sexual dimorphism is also of concern to the systematic malacologist and paleontologist. Most gastropod taxonomy at the species level is based on shell-shape characters. If sexual dimorphism is present and subtle, the probability of confusing a single species as two different species is remote. However, if the sexual dimorphism is extreme, the possibility of confusion is high. For Recent species, the discovery of two morphologically similar congenerics, each composed of a single sex, would provide evidence that extreme sexual dimorphism was present. However, for paleontologists who do not have the benefits of soft-part anatomy, recognizing extreme sexual dimorphism in shell shape may be nearly impossible. Moreover, the lack of soft-part anatomy could lead to confusion on the generic level, given the paleontologist's total reliance on shell characters.

Most of the previous methods that have been used to quantify and analyze shape differences between male and female gastropods have used bivariate data plots and frequency histograms. These data typically consist of ratios between linear shell measurements [chosen by the author(s)] and, if treated statistically, they employ parametric tests of significance such as the Student's t-test.

The many different ratios that have been used to quantify gastropod shell shape make it difficult to make comparisons between taxa and to recognize patterns in the evolution of shell dimorphism. Standardized measurements would facilitate comparisons and provide an important data base for studies of sexual dimorphism. The parameters used by Raup (1966),

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Vermeij (1973) and Verduin (1983) to describe gastropod shell shape are available and could provide standard data sets for analysis.

Statistical analysis and tests of significance need to be rigorous. Certain multivariant analyses are particularly well suited for identifying morphological differences (see Reyment, 1969). Discriminant function analysis is especially useful because it not only identifies those variables that discriminate between groups (i.e., males and females), but it also can classify ungrouped specimens based on the results from known groups.

In this paper, shell parameters (Raup, 1966; see also Kohn & Riggs, 1975) of male and female specimens of the sexually dimorphic *Margarites vorticifera* (Dall 1873) were measured and entered into a discriminant function analysis to determine the parameter(s) responsible for the shell dimorphism. I then measured the type material of the four synonyms of this species and performed the analysis with these data ungrouped, because soft-part anatomy was not available for the type specimens. The results of these analyses and a discussion of the variables that caused taxonomic confusion in this species are presented.

Abbreviations used herein are as follows: ANSP, Academy of Natural Sciences, Philadelphia; CASIZ, Department of Invertebrate Zoology, California Academy of Sciences, San Francisco; NMNS, National Museum of Natural Sciences, Ottawa, Canada; SU, Stanford University type collection (now on permanent loan to CASIZ); UCMP, Museum of Paleontology, University of California, Berkeley; USNM, U.S. National Museum of Natural Sciences, Washington.

MATERIALS AND METHODS

Specimens of the trochid gastropod *Margarites vorticifera* were collected at a depth of 7 m near the entrance of Chichagof Harbor, Attu Island, Alaska (52°56′N, 173°14′E). *M. vorticifera* is a brooding species and the developing embryos are held in the umbilicus of the female shell. The volume of the female shell is about 1.5 times greater than the volume of the male shell in the larger size classes (Lindberg & Dobberteen, 1981) (Fig. 1). A total of nine female shells and seven male shells were measured.

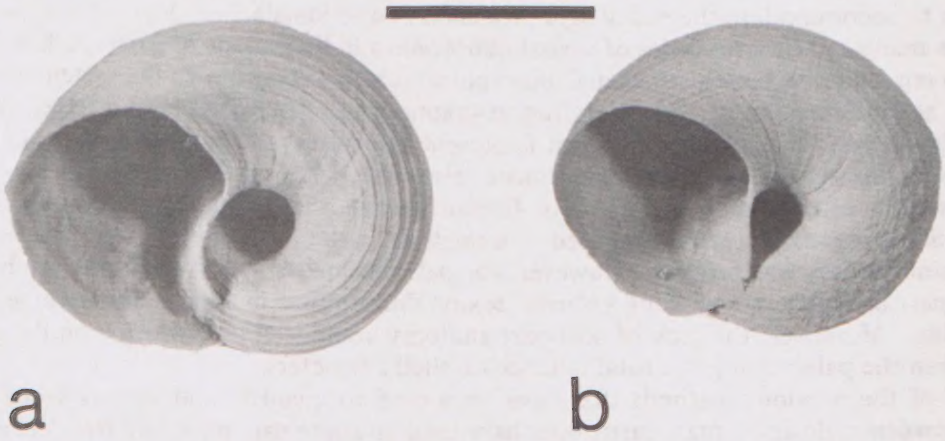

FIG. 1. Umbilical views of *Margarites vorticifera*. a, Female (UCMP 37484); b, male (UCMP 37434). Bar = 10 mm.

Four names have been proposed for this species: *Margarites vorticifera, M. sharpii* (Pilsbry 1898), *M. ecarinatus* Dall 1919, and *M. avenosooki* MacGinitie 1959. Primary type material of each species was borrowed (except for *M. ecarinatus*, for which photographs were furnished) and measured.

Measurements were not taken directly from the shell but from *camera lucida* drawings that were prepared with the shells in a standard orientation (Fig. 2). Ten measurements were needed to determine the four parameters [position of generating curve (D), whorl expansion rate (W), whorl translation (T), and

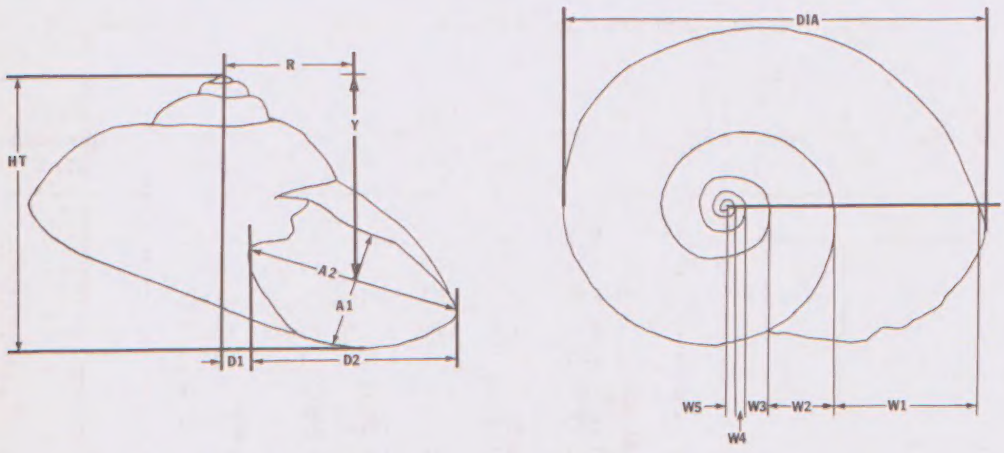

FIG. 2. *Camera lucida* drawings of *Margarites vorticifera* in standard orientations, showing linear measurements used to calculate shell parameters.

Abbreviations: A = aperture; D = position of generating curve; DIA = maximum diameter; HT = shell height; R = radius; W = whorl; Y = translation.

TABLE 1. Derivation of shell parameters.

Variable	Linear measurements (from Fig. 2)
S	A1/A2
W	$\frac{W2/W1 + W3/W2 \ldots + Wn/Wn\text{-}1}{n - 1}$
D	D1/D2
T	Y/R

Abbreviations: A = apertural dimension; D = position of generating curve; R = radius; S = apertural shape; T = whorl translation; W = whorl expansion rate; Y = translation.

apertural shape (S)] used in this study; maximum diameter (DIA) and height (HT) of each shell also were measured (Fig. 2; Table 1). The data used in the discriminant function analysis are presented in Table 2.

The data set was analyzed with the discriminant function analysis program of the Statistical Package for the Social Sciences (SPSS) (Nie et al., 1975). Although a total of 23 cases were entered, the type material was excluded from the analysis for shape differences because their sex was unknown. However, they were included in the classification phase of the program so that probable sex could be determined by comparing their shell parameters to those of the sexed shells. In a recent paper, Shaklee & Tamaru (1981) have provided an excellent discussion of the strengths and weaknesses of discriminant function analysis with these types of data.

TABLE 2. Variables and groupings used in discriminant analysis in *Margarites*.

Species	Sex	No.	Variable						Type specimen data
			S	W	D	T	HT	DIA	
M. vorticifera	female	1	.577	.467	.157	1.45	11.92	17.00	
		2	.588	.455	.113	1.73	11.50	16.42	
		3	.633	.443	.167	1.64	10.50	14.33	
		4	.492	.503	.158	1.55	12.67	18.50	
		5	.542	.473	.125	1.77	11.67	17.83	
		6	.641	.492	.177	1.38	10.83	17.33	
		7	.519	.446	.153	1.65	11.92	18.33	
		8	.431	.432	.145	1.56	11.67	18.17	
		9	.550	.426	.095	1.73	14.33	20.50	
	male	1	.530	.497	.081	1.76	12.50	19.00	
		2	.517	.504	.067	1.94	12.60	18.33	
		3	.560	.548	.074	2.29	12.00	15.33	
		4	.580	.586	.061	2.53	12.33	16.25	
		5	.473	.555	.071	1.83	11.50	17.50	
		6	.644	.458	.067	2.22	10.92	14.17	
		7	.575	.470	.057	2.22	10.42	14.00	
	?	1	.670	.609	.122	2.43	12.73	14.00	Holotype; USNM 606374
M. sharpii	?	1	.610	.460	.201	1.40	9.25	14.08	Syntype; ANSP 70554
	?	2	.698	.521	.208	1.55	7.92	10.75	Syntype; ANSP 70554
	?	3	.617	.494	.200	1.50	5.75	7.67	Syntype; ANSP 70554
M. avensooki	?	1	.750	.660	.142	1.28	8.90	11.70	Holotype; USNM 126758
	?	2	.793	.417	.219	1.59	8.08	10.25	Paratype; SU 8331
M. ecarinatus	?	1	.500	.630	.260	8.60	8.00	15.75	Holotype; NMNS 4071

Abbreviations: D = position of generating curve; DIA = maximum diameter; HT = height; S = apertural shape; T = whorl translation; W = whorl expansion rate.

RESULTS

The four shell parameters used in the analysis produced a very high degree of separation between the shells of known male and female *Margarites vorticifera* (canonical correlation = .9230) (Fig. 3). The combination of positive and negative coefficients indicates that the differences between male and female shells are not due to size, but represent differences in shape

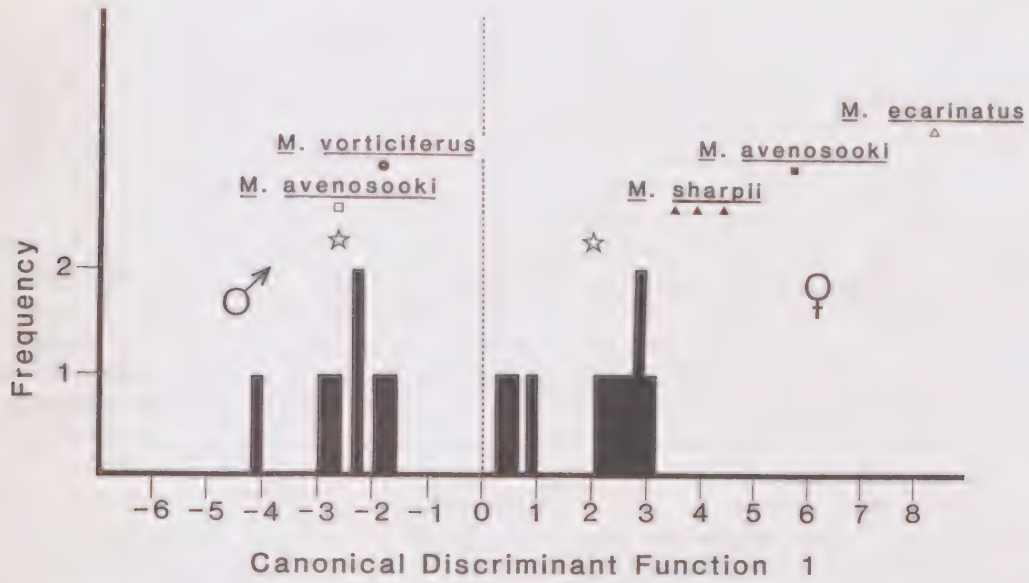

FIG. 3. Frequency histogram of individual discriminant scores for male and female specimens of *Margarites vorticifera*. Type material, plotted above histogram, entered as ungrouped data.
* = group centroid.

(Table 3). The position of the generating curve in relation to the axis (D) and the whorl expansion rate (W) are three to five times more important than the other parameters for discriminating between male and female shells, and apertural shape (S) is about twice as important as the rate of whorl translation (T). In female shells, D and T are relatively greater than W and S; the reverse situation is indicated in male shells.

TABLE 3. Standardized canonical discriminant function coefficients.

Function	Variable			
	D	T	W	S
1	1.044	0.098	-0.659	-0.229

Abbreviations: D = position of generating curve; S = apertural shape; T = whorl translation; W = whorl expansion rate.

The results of the classification of the ungrouped type material also are presented in Fig. 3. The holotype of *Margarites vorticifera* was classified as a male shell ($\underline{P}$ = .99). The three syntypes of *M. sharpii* all were classified as female shells (P. = 1.0, 1.0, 1.0), as was the holotype of *M. ecarinatus* ($\underline{P}$ = 1.0). The classification of types of *M. avensooki* provided interesting results. The holotype was classified as a male ($\underline{P}$ = 1.0) while the paratype was classified as a female shell ($\underline{P}$ = 1.0).

DISCUSSION

Shell sexual dimorphism in *Margarites vorticifera* appears to be primarily a result of changes in the position of the generating curve in relation to the shell axis and, to a lesser extent, due to changes in the whorl expansion rate (D is about 1.5 times more important than W). In some cases, these are the very same characters that the authors of the synonyms used to distinguish their species from *M. vorticifera*.

In the original description of *Margarites vorticifera*, Dall (1875: 59) compared *M. vorticifera* to the circumarctic and boreal species *M. helicinus* (Phipps 1774), noting that they were "widely differing in characters." The specimen that Dall illustrated (pl. II, figs. 4, 4a, 4b) has the characteristics of a male shell and, when parameters taken from the figure are entered into the discriminant analysis as an unclassified specimen, it is classified as a male shell ($\underline{P} = .77$). However, the figured specimen and the holotype do not appear to be the same specimen.

Pilsbry (1898: 486) described *Margarites sharpii* from material from Dutch Harbor, Unalaska, Alaska. He compared the new nominal species to *M. vorticifera*, noting that the two species resembled each other in "color, texture, and sculpture," but differed in whorl expansion rate, size of the umbilicus and position of the parietal wall. All of these characters are clearly related to the sexual dimorphism and, with the exception of the parietal wall, are the very same characters identified by the discriminant function analysis as the discriminating characters between male and female shells. The discriminating ability of Henry A. Pilsbry's eye was quite good.

The two remaining nominal species, *Margarites ecarinatus* and *M. avensooki*, do not appear to be based on sexual dimorphic characters. Dall (1919) compared *M. ecarinatus* to *M. vorticifera*, noting differences in translation, whorl shape and sculpture. *M. avensooki* was described without comparisons to other taxa, and the type material consists of both male and female specimens of *M. vorticifera*. The shell parameters of the holotype place it almost exactly at the group centroid for male specimens, while the paratype is distinctly a female shell. Thus, the criteria that distinguish *M. avensooki* from other *Margarites* species are unknown and the sexual dimorphism present in the type material went unnoticed.

Sexual dimorphism in *Margarites vorticifera* is also partly responsible for the proposing of a taxon at the generic level. Habe & Ito (1965: 30) proposed the genus *Omphalomargarites* for *M. vorticifera*, because it was, in their view, quite different from other members of the genus *Pupillaria* (Dall, 1909) in which *M. vorticifera* is often placed. The differences included a thin and low shell, the oblique aperture, and the "extremely large body whorl with the widely opened umbilicus." These last two characters are directly related to the sexual dimorphism in this species and, using their criteria, male and female specimens of *M. vorticifera* could be placed in different genera.

This type of taxonomic confusion would be even more likely in fossil species that had extreme sexual dimorphism, because of the problems of preservation of shell detail and the inherent difficulties of working with molds and casts. The presence of two distinct morphotypes in a population of fossil gastropods is compelling evidence of sexual dimorphism, especially when they are present in an approximate 1 to 1 ratio (see Linsley, 1978). Subsequent multivariant analysis of the two fossil groups, using standardized shell parameters, could identify those parameters that contribute to the morphological differences.

In the present study, discriminant function analysis was used to correlate soft-part anatomy (sex) with hard-part morphology. This technique is especially well suited for mollusks, because their basic morphologies can be described by specified parameters. These parameters are easily determined for most Recent and even fossil species. Moreover, there are extensive museum collections of mollusk shells available for analysis once a unique anatomical character is associated with certain shell parameters. Discriminant function analysis can be used to select the single specimen in a lot that is closest to the group centroid for the population

under study. Even illustrations can be used if there are sufficient views to characterize fully the specimen.

Outside of the Mollusca, discriminant function analysis has been used to determine the identity of type material of Hawaiian bonefishes. Shaklee & Tamaru (1981) first identified two species of bonefish biochemically. Morphological characters of the two species were then used in a discriminant function analysis to distinguish the two species morphologically. Lastly, the type material of a third nominal species was measured and entered into the analysis as ungrouped, thus allowing it to be compared to and classified with the knowns. Their resulting classification clearly showed that the holotype was one species while the paratype was the other species. This was done with reasonable certainty for museum specimens for which the biochemical data were unretrievable. Similar approaches to taxonomic problems in the Mollusca, where biochemical data are available for modern populations and the type material of the nominal species consists only of shells, should prove successful.

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DEFENSIVE BEHAVIOR IN LITTORAL SNAILS FROM LEBANON[1]

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ABSTRACT

The defensive reactions of three littoral snails, *Littorina neritoides, L. punctata* and *Monodonta mutabilis* were tested. Crushed conspecifics, a passing prawn (*Palaemon elegans*) and the passing of a large shadow were offered as stimuli. *L. neritoides* and *L. punctata* were more likely to hide in a complex environment when in the presence of a crushed conspecific than under control conditions. All *M. mutabilis* withdrew their tentacles in response to a large passing shadow, but *L. neritoides* and *L. punctata* usually failed to respond. All species responded negatively to *P. elegans* as a stimulus. Species-specific differences in response were rationalized by considering ecological factors.

INTRODUCTION

All aquatic animals are sensitive to different degrees of chemical changes in their environment. Chemoreception plays an important role, in conjunction with the other senses, in widening an animal's sensory field and environmental awareness, but it remains the least understood of all these senses (Nichol, 1960). Most molluscs, as well as the majority of other animals, find their food, locate their mates, detect their homes and avoid their enemies by chemoreception (Kohn, 1961). Chemically mediated responses to enemies can be divided into two categories, depending on the nature of the stimulus: avoidance responses initiated by chemicals issued from the predators and escape responses triggered by contact with the predator (Phillips, 1977). For many gastropods, tissue juices from crushed conspecifics will trigger avoidance responses (Synder & Synder, 1971; Ashkenas & Atema, 1978; Hadlock, 1980).

Lucas (1947) hypothesized an ectocrine theory, where external metabolites produced by some members of an aquatic community affected the behavior of the other members. Bullock (1953) suggested an inclusion of predator-prey relationships because some molluscs can sense potential predators at a considerable distance (Feder, 1963; Synder & Synder, 1971; Phillips, 1975; Ashkenas & Atema, 1978; Hadlock, 1980; McKillip, 1982).

Life within the Mediterranean intertidal zones is harsh, with species in continual competition. Predator-prey relationships are in operation, yet we find relatively few empty shells for three species of gastropods, *Littorina neritoides* (Linné), *L. punctata* (Gmelin) and *Monodonta mutabilis* (Philippi).

Littorina neritoides is common throughout the Mediterranean. It exists in deep crevices in the upper part of the shore above mean high water neaps (MHWN) and is never encountered in any large numbers below MHWN (Underwood, 1973). Southward (1958) has found them in the supra-littoral fringe, which in the Mediterranean is usually situated above the normal upper limits of the tide, and associated with lichens. *L. neritoides* is best represented on steep, rough and very exposed surfaces and is reduced in numbers within semi-exposed localities (Lysaght, 1941; Evans, 1947). Palant & Fishelson (1968) described the Levantine environment of *L. neritoides* and *L. punctata* as being restricted to exposed areas sheltered from waves and having limited macro-algae cover.

Next to *Littorina neritoides*, the most common mollusk in the Mediterranean is *Monodonta turbinata* (Peres & Picard, 1964). *M. turbinata* are limited to a tidal range that does not exceed

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30 to 60 cm (Luther & Fiedler, 1976). They are common on the uppermost level of the intertidal zone, but extend their range into the surf or splash zone, where they experience a maximum of 60-70% aerial exposure (Houlihan & Innes, 1982). We find that *M. mutabilis* occupies similar habitats like those described for *M. turbinata*. We have observed *M. mutabilis* usually to be submerged in tidal pools or on sheltered, bare and moist rock surfaces near the water line.

We are interested in learning more about the behavior of these three species. *Littorina neritoides* and *L. punctata* are found together in mixed clusters within crevices of rocks, but do not overlap habitats with *Monodonta mutabilis*. One would assume that these snails have different behaviors, which enhance their survival and place in the environment. We emphasize in this study their different avoidance responses to crushed conspecifics, a large passing shadow and moving prawns.

MATERIALS AND METHODS

Monodonta mutabilis were collected from the American University of Beirut beach in Ras Beirut. *Littorina neritoides* and *L. punctata* were collected from the University beach and near Jounieh, Lebanon. Voucher specimens have been deposited in the collections of the U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A. (catalogue nos. 836264-836266). *L. neritoides* and *L. punctata* were maintained in culture dishes and the water was changed every four days, while *M. mutabilis* were kept in large tanks. We administered three types of stimuli: crushed snails, large passing shadow and prawn movement. Each individual snail was used only once. The temperature in the laboratory ranged between 21-23°C. We observed concurrently the blanks and the addition of 5 or 10 ml of sea water. Activities for study included: the time taken for the snails to crawl out of water, the direction of movement, tentacle movement, and hiding. We avoided additional vibrations of the table or shading the snails because either phenomenon affected snail activity.

We did not separate *Littorina neritoides* and *L. punctata* for individual series of observations or testing. We chose to study their responses in a collective fashion in accordance with their ecological concurrence. Hereafter they are referred to as *Littorina*. For *Littorina*, tests were run in culture dishes containing water 4 cm deep and were introduced individually into the culture dishes just before the experiments were started. Acclimation for these snails was not possible because of their behavior. Crushed conspecifics or 5 ml of sea water were added after the snails had started climbing the water column. The number of crushed snails ranged from 1 to 25, and in each case the snails were crushed thoroughly in a mortar with 5 ml of sea water. Hiding response times from crushed snails were determined as the time required for a snail to crawl beneath a portion of laboratory tubing 2.5 cm in length, 1 cm internal diameter and wrapped in aluminum foil. We also recorded the duration of hiding.

We performed the *Monodonta mutabilis* tests in glass carboys containing 1.5 l of water to a height of 11 cm. *M. mutabilis* were introduced individually at least one hour before experiments were started. Those *M. mutabilis* which crawled out of the water before one hour had passed were not used. One to five crushed *M. mutabilis* or 10 ml of sea water were added when the snails were either on the water line, climbing midway along the water column or still crawling at the bottom. We recorded the position of the snail at the beginning of the observation period (20 to 75 min) and at its end. The aim was to determine the direction of any escape response. We terminated observations when the snail exited the water. The total distance travelled by each snail and the time taken to do so were recorded.

We studied the effect of large passing shadows on tentacle extension and snail movement. Experimental animals were illuminated (150 foot candles at water surface) and a black cardboard was passed quickly over them. A recently killed prawn, *Palaemon elegans* (Rathke), attached to the tip of a probe was introduced into the water with minimal disturbance of the water and passed in front of the snail species to study its effect on tentacle extension and snail movement. Water disturbance always ended in withdrawal of tentacles and cessation of movement.

All data were analyzed using the methods of Steel & Torrie (1960).

RESULTS

Avoidance reactions of *Littorina* and *Monodonta mutabilis* to experimental stimuli were expected to be either a drop to the bottom, thus blending into the substrate, or an exit from water, if the source of danger was within the water.

In blank experiments, *Littorina* moved directly from the bottom of the culture dishes and out of the water, clustered themselves above the water line and remained stationary. When

Littorina were crawling out of the water with their tentacles extended, the addition of 5 ml sea water or crushed conspecifics resulted in momentary withdrawal of tentacles and cessation of snail movement. The addition of 5 ml sea water had no effect on the direction of movement out of the water, but the addition of crushed conspecifics resulted in disorientation of movement, whereby the snail either moved back and forth along the side of the culture dish before leaving the water column or moved horizontally before reorientating itself. This was reflected in the time taken for *Littorina* to leave the water. Analysis of variance demonstrated that the addition of crushed conspecifics had an effect ($P < 0.05$) when compared to blank and sea water addition treatments ($F = 11.1$, $df = 2.74$). The average time to exit the water was 2.9 ± 1.2 (SD) min for blanks, 3.1 ± 1.1 (SD) min for sea water additions and 7.2 ± 6.1 (SD) min for addition of crushed conspecifics.

Whether the observed upward and downward movement was an escape out of the water or towards the bottom was difficult to determine. Fig. 1 indicates that with the increase in the number of crushed conspecifics there was a decrease in the escape time. Regression analysis demonstrated a significant relationship ($t = 4.37$, $df = 24$) between the time for *Littorina* to crawl out of the water and the number of crushed conspecifics, but no threshold for the response could be determined.

Hiding behavior as time to find refuge, when a piece of laboratory tubing was offered, averaged 2.7 ± 1.4 (SD) min for blanks; for crushed conspecifics, 3.8 ± 1.7 (SD) min; and for sea water, 4.0 ± 1.8 (SD) min. Average duration for hiding was 13.4 ± 6.2 (SD) min and ranged between 4 to 26 min. No significance ($P = 0.05$) was found for any of these hiding behaviors when the data were quantified.

The passing of a large shadow resulted in momentary withdrawal of tentacles, and hence in cessation of movement, in only 16 out of 100 *Littorina*. The passing of *Palaemon elegans* without disturbance of water had no effect on the snails' tentacle extension or movement in 50 cases.

With *Monodonta mutabilis*, it was not easy to follow the direction of movement. Contrary to *Littorina*, whose movement was directly out of the water and was affected by adding crushed conspecifics, *M. mutabilis* movement under situations when sea water or when crushed conspecifics were added included upward and downward movements below the water line. This movement was expressed as the total vertical distance travelled divided by the time taken

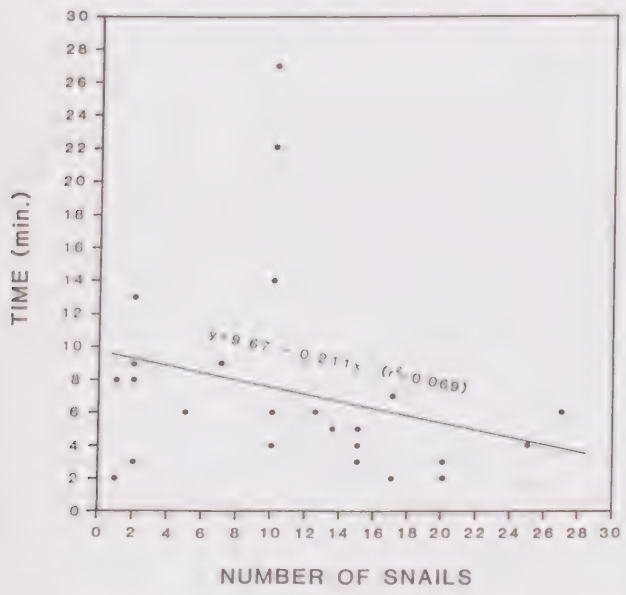

FIG. 1. Numbers of added crushed conspecifics versus the time taken by *Littorina* to exit the sea water.

TABLE 1. Rates of crawling for *Monodonta mutabilis*. Mean crawling is expressed as cm moved/min. Six observations were made for each treatment.

Experimental treatments	Rates including non-movement	Rates without non-movement
Blank	1.13	1.70
10 ml sea water	0.94	1.71
1 crushed conspecific	5.66	5.66
2 crushed conspecifics	2.68	2.68
3 crushed conspecifics	2.12	2.55
4 crushed conspecifics	1.62	1.95
5 crushed conspecifics	3.06	3.63

to travel this distance (Table 1). Time of non-movement was excluded. No statistical significance ($P = 0.05$) for rates of movement could be found for the addition of crushed snails in comparison to the treatments for blanks and sea water addition treatments.

We determined the amount of time between the start of the experiment and the first response (either extension of tentacles or start of movement) on the snails investigated. No significance ($P = 0.05$) may be ascribed to their responses for our test stimuli. The passing of a large shadow resulted in momentary withdrawal of tentacles and cessation of movement in all cases. The passing of *Palaemon elegans* without disturbance of water had no effect on tentacle withdrawal or movement. *Monodonta mutabilis* demonstrated no hiding behavior.

DISCUSSION

When put at the bottom of culture dishes, *Littorina* crawled directly out of the water. This was in agreement with Underwood's (1972) study of tide-model analysis for the zonation of four *Littorina* species. He found that *L. neritoides* crawled rapidly upward until they reached above high-water level. They became motionless, unless splashed with sea water. This behavioral pattern was modified with our addition of crushed conspecifics, which resulted in disorientation of *Littorina* movement. The backward and forward movement along the water column resulted in a long exit time as compared to the exit time for blanks or for the additions of sea water. It appeared that the snails were searching for a hiding place. We did not observe this movement when laboratory tubing was introduced as an artificial refuge. Hadlock (1980) found that, upon the addition of juices from crushed conspecifics, *L. littorea* responded by increasing crawling velocities and by moving towards rock crevices or under macro-algal fronds. This was comparable to our results where the average time needed for *Littorina* to cover the distance from the middle of the culture dish to a piece of laboratory tubing was fastest for crushed conspecifics, in comparison to blanks and sea water addition.

Synder & Synder (1971), Phillips (1977) and Hadlock (1980) found that the majority of gastropods responded to crushed conspecifics by hiding or by self-burial. The adaptive advantage of hiding is not immediately apparent because they are slow crawlers. Hadlock (1980) suggested a hypothesis based on the feeding behavior of *Carcinus maenas* and the hiding response of *Littorina littorea*. She found that individuals of *L. littorea* needed 10 min to hide, a period required by *C. maenas* to devour a medium-sized snail. As a snail was eaten, the other snails gained time to hide or to distance themselves from the predator. Hadlock (1980) concluded that the alarm response of the intertidal snail *L. littorea* was an adaptation to the feeding behavior of the predator crab *C. maenas*. This response to feeding might be compared to the response of moths for echo-locating bats (Roeder & Treat, 1961). The alarm response of a prey organism is an adaptation to predatory feeding.

Monodonta mutabilis failed to have any obvious avoidance response to crushed conspecifics, in contrast to *Littorina*. *M. mutabilis* may be too large and hard-shelled to be eaten by anything in the small splash pools. It may be removed to an anvil area, smashed and eaten. However, *Littorina* are small, have fragile shells, and could be eaten near the capture site. Hence, body fluids of *M. mutabilis* would rarely flow into the water serving as a potential warning stimulus to conspecifics, in contrast to *Littorina*. Unfortunately, it was not possible to test the avian predation risk in Lebanon, since almost all the wading birds have been shot or poisoned by inappropriate local use of pesticides.

Littorina consistently failed to withdraw into their shells when a large shadow passed over, but *Monodonta mutabilis* always did. This disparity can be rationalized if one considers that large shadows mimic that produced by a wading bird. Yet all snails moved slowly that none of the species could hide quickly from such a bird. However, birds would present a greater risk to *M. mutabilis*, since they may represent a greater potential resource to the predator (Goss-Custard, 1977). It was possible that *Littorina* was an unpalatable prey to the local birds, but Hadlock's (1980) work with crabs showed *L. littorea* to be palatable. Unpalatable prey were less likely to attempt escape than were palatable prey (Evans, 1983). Their black shell color might be interpreted as being aposematic.

None of the species responded to the passing of dead *Palaemon elegans*. Living *P. elegans* will move towards a snail or any other small object dropped into a splash pool and will attempt to feed on it; however, since all species spend considerable time above the mean pool level, *P. elegans* predation is seemingly a negligible factor in the lives of these snails.

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ENZYME ANALYSES OF *BITHYNIA* (MOLLUSCA: BITHYNIIDAE) BY ISOELECTRICFOCUSING[1]

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ABSTRACT

Isoenzymes of *Bithynia funiculata, B. siamensis* and *B. s. goniomphalos* were analysed by isoelectricfocusing in polyacrylamide gel. The enzymes studied were: carbonic anhydrase, alkaline phosphatase, lactic dehydrogenase, acid phosphatase, phosphoglucoisomerase, malate dehydrogenase, phosphoglucomutase, glutamate-oxaloacetate transaminase, hexokinase, glutamate dehydrogenase, leucine aminopeptidase and esterase. Genotypic differences between the two species were detected in four enzyme systems: lactic dehydrogenase, phosphoglucomutase, phosphoglucoisomerase and esterase. The data provide strong evidence for the species status of *B. funiculata* and *B. siamensis*. The two subspecies of *B. siamensis* differed in esterase isoenzyme types. Each snail species and subspecies has its own specific enzyme types distinguishable by the biochemical method.

INTRODUCTION

Two species and one subspecies of freshwater snails of the genus *Bithynia* have been reported to be the natural intermediate hosts of *Opisthorchis viverrini* (Poirier) in Thailand. They are *Bithynia funiculata* Walker, *B. siamensis siamensis* Lea and *B. s. goniomphalos* Morelet (Brandt, 1974). *B. s. goniomphalos* is endemic in northeast Thailand, *B. s. siamensis* in central Thailand and *B. funiculata* in north Thailand. Systematic identification between species and subspecies is difficult due to their morphological similarity and variability. Although some populations have clear-cut characters, many possess intermediate characters among these species.

The application of the technique of isoenzyme electrophoresis to aid in solving taxonomic problems is now well accepted (Davis, 1967; Rollinson & Southgate, 1979; Wurzinger, 1979; Fletcher et al., 1980; Kreutzer & Sousa, 1981; Kitikoon, 1982; Chung, 1984). The present study was undertaken to establish whether *Bithynia funiculata, B. siamensis siamensis* and *B. s. goniomphalos*, collected from their natural habitats, could be distinguished by their enzyme types and whether the biochemical method would help to determine the systematic relationships among these snail species.

MATERIALS AND METHODS

Snails were collected from various locations in their natural habitats, identified and set up for cercarial shedding. Uninfected snails were kept and maintained in the laboratory at the Center for Applied Malacology and Entomology, Faculty of Science, Mahidol University, Bangkok. Only mature snails of similar size were selected for this study. Before they were used for the experiments, the shells were gently cracked to expose the snail bodies which were later removed and ground individually in 0.3 ml of 0.1 M glycine buffer (pH 7.2) in an ice-bath using a small tissue grinder. The snail suspensions were later sonicated three times for 20 sec each at 150 w (Lab-Line Instrument, Inc.) and centrifuged at 12,000 rpm for 30 min at 4-6°C. The clear supernates were collected and stored at –70°C until used.

The LKB multiphor system (LKB-Produkter, Sweden) was used in this study. Isoelectricfocusing of the enzyme types was performed on thin (0.1 cm) layers of 4.8% polyacrylamide gel using Ampholine as

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carrier ampholytes. All enzymes were separated on pH 5-8 gels. The homogenate of individual snails was absorbed on a piece of 4 x 10 mm Whatman filter paper No. 3 and placed on the gel slab about 5 mm apart. Twenty-four samples of snail species and subspecies were applied for each electrophoresis run. The gel was pre-run at 50 mA for 45 min before the filter papers were removed. Horizontal electrofocusing was continued at 1200 v for 3 hr. The pH gradient of the gel was measured every 1.0 cm by means of a surface electrode. The numbers of snails used for analyses from each species and subspecies were between 36 and 48.

Twelve enzymes were analysed. They were: carbonic anhydrase (CA), alkaline phosphatase (ALP), lactic dehydrogenase (LDH), acid phosphatase (ACP), phosphoglucoisomerase (PGI), malate dehydrogenase (MDH), phosphoglucomutase (PGM), glutamate-oxaloacetate transaminase (GOT), hexokinase (HK), glutamate dehydrogenase (GDH), leucine aminopeptidase (LAP) and esterase (EST). The techniques used for detecting these enzyme activities were from Brewer (1970), Steiner & Joslyn (1979) and Gaal et al. (1980), with some modifications. The substrate used for detection of esterases was α-naphthyl acetate. Unless otherwise stated, all chemicals used for enzyme analyses were from Sigma Chemical Co.

For comparisons between species and subspecies, snail extracts were electrophoresed on the same gel. The isoenzyme pattern is related to a pH gradient across the gel and the individual fractions are separated at their isoelectric points (pI). Comparisons were based on the difference of the number of fractions and their pI values.

Voucher specimens have been deposited in the Museum of Malacology and Entomology, Mahidol University (voucher catalogue nos. MUFS 007 to MUFS 009).

RESULTS

The enzyme types were distinguished by the patterns of their activities in the stained gel. Because the isoenzymes are localized at their pI values, comparison between species and subspecies was based on the differing pI values of the bands which also reflected the number of loci involved. The snail sexes were not determined; however, the individual snails were analysed and only slight variation on the patterns of major enzyme loci within species and subspecies was detected in this study. Of the 12 enzymes examined, consistent and interpretable patterns of isoenzymes were observed in eight systems. Interspecific variations were detected in four enzymes: LDH, PGM, PGI and EST. The comparative schematic diagrams of the electrophoretic phenotypes of the snail species and subspecies are demonstrated in Figs. 1, 2 and 4.

Lactate dehydrogenase

Similar patterns of isoenzymes were detected in *Bithynia siamensis goniomphalos* and *B. s. siamensis*. A single faint band was found to have a pI value of 6.7, while the other two well-defined bands were close together at the pI values of 7.3 and 7.5 respectively. *B. funiculata*

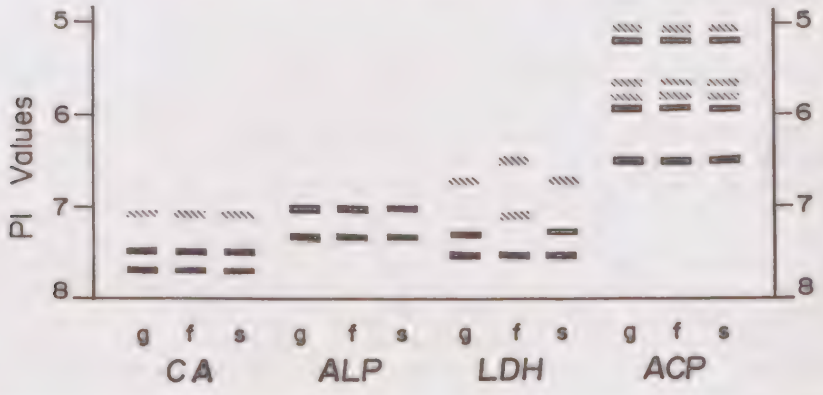

FIG. 1. Schematic comparisons of electrophoretic patterns of carbonic anhydrase (CA), alkaline phosphatase (ALP), lactic dehydrogenase (LDH) and acid phosphatase (ACP). g = *Bithynia siamensis goniomphalos*, f = *B. funiculata* and s = *B. s. siamensis.*

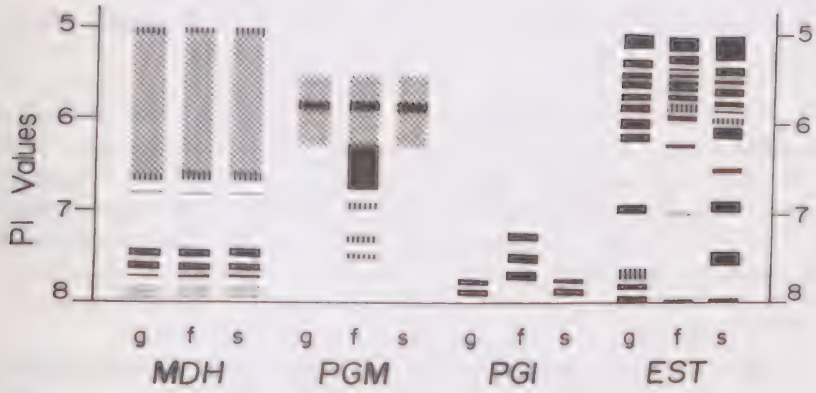

FIG. 2. Schematic comparisons of electrophoretic patterns of malate dehydrogenase (MDH), phosphoglucomutase (PGM), phosphoglucoisomerase (PGI) and esterase (EST). See Fig. 1 for further abbreviations.

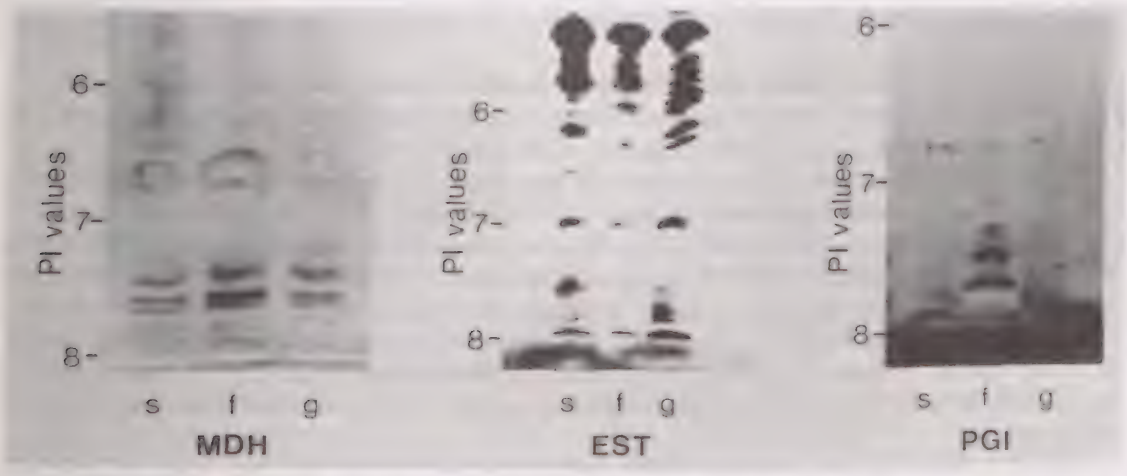

FIG. 3. Photographs of electrophoretic patterns of malate dehydrogenase (MDH), esterase (EST) and phosphoglucoisomerase (PGI). See Fig. 1 for further abbreviations.

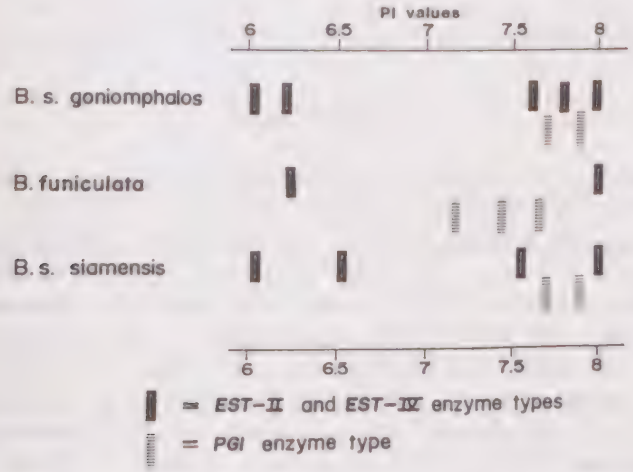

FIG. 4. Diagrammatic representation of specific electrophoretic patterns of *Bithynia siamensis goniomphalos*, *B. funiculata* and *B. s. siamensis* on esterase (EST)-II, EST-IV and phosphoglucoisomerase (PGI).

differed in that it showed three bands of enzyme activity at the pI values of 6.6, 7.2 and 7.5.

Phosphoglucomutase

Three loci were estimated in this isoenzyme system. PGM-1 appeared as a well-stained band at the pI value of 5.8. A smear zone covered the area between pH 5.5 to 6.3 on the gel. No variation was detected between snail species and subspecies. PGM-2 appeared as a broad, well-stained band between pH 6.3-6.7 on the gel. PGM-3 was composed of three faint bands at the pI values of 6.9, 7.3 and 7.5 respectively. PGM-2 and PGM-3 were found to be species specific for *Bithynia funiculata*.

Phosphoglucoisomerase

Evidence for species-specific isoenzyme patterns was clearly demonstrated in PGI. Two loci were detected between pH 7 and 8 of the gel. PGI-1 appeared as two well-defined bands of the pI values of 7.7 and 7.8. PGI-2 was composed of three well-stained bands at the pI values of 7.3, 7.5 and 7.7 respectively. *Bithynia siamensis siamensis* and *B. s. goniomphalos* were found to have the PGI-1 locus, while only the PGI-2 locus was detected in *B. funiculata*.

Esterase

Interspecies and intraspecies variations were detected in the nonspecific esterase isoenzyme patterns. Four distinct zones of activities were consistently observed and were assigned as four presumptive genetic loci, namely, EST-1, EST-2, EST-3 and EST-4.

EST-1. The differences between species and subspecies of snails could be noticed from the isoenzyme patterns which occurred between pH 5 and 6 of the gel. Six well-defined bands of enzyme activities were clearly detected in *Bithynia siamensis goniomphalos*, but the bands were rather compacted and difficult to differentiate in *B. s. siamensis* and *B. funiculata*.

EST-2. Variation of the isoenzymes was clearly detected by the difference of the number of electromorphs and their pI values. A single well-defined band of enzyme activity was resolved at the pI value of 6.3 for *Bithynia funiculata*, while two bands of pI 6.0 and 6.2 were detected in *B. siamensis goniomphalos*, and two bands of pI 6.0 and 6.5 were found in *B. s. siamensis*.

EST-3. All populations of snails were found to have a single band, although of different widths, at pH 7 of the gel.

EST-4. Variation between species and subspecies was clearly demonstrated in this locus. *Bithynia funiculata* had one band of enzyme activity at the pI value of 8, while *B. siamensis siamensis* had two bands of pI values 7.5 and 8.0, and *B. s. goniomphalos* contained two well-defined bands at pI 7.8 and 8.0 and a diffused band at the pI value 7.7.

DISCUSSION

Enzyme electrophoresis is a convenient method for studying genetic relationships between population and species (Davis & Lindsay, 1967; Coles, 1970; Fletcher et al., 1980; Kreutzer & Sousa, 1981; Tibayrent & Miles, 1983). This technique has been used by many workers for aid in clarifying the taxonomic problems of snails (Rollinson & Southgate, 1979; Wurzinger, 1979; Kitikoon, 1982). The *Bithynia* snails examined in this study are morphologically similar; however, they were isolated geographically. To understand relationships between the snail populations and species, it is necessary to assess how different they are genetically and how much variation exists. The snails examined in this study were primarily identified by using morphological criteria. The enzyme data obtained from this experiment has supported the systematic criteria. The differences between species of *Bithynia funiculata* and *B. siamensis* were found to be greater than the differences between the subspecies *B. s. siamensis* and *B. s. goniomphalos*.

There are four distinct enzyme groups of *Bithynia funiculata* which have been demonstrated to have isoenzyme patterns different from those of *B. siamensis*. Of particular interest is when two major isoenzyme patterns (PGI and EST) were compared and well-defined bands occurring between pH 6-8 of the gel were used for characterization. The unique isoenzyme pattern of *B. funiculata* supports the evidence of geographic and taxonomic separation of this snail species from *B. siamensis*.

The major differences between species were detected in PGI, PGM and EST, especially on the PGI-1, PGI-2, EST-1 and EST-4 loci. As shown in Fig. 4, the specific PGI-1 enzyme type of *Bithynia funiculata* was clearly distinct from PGI-2 of *B. siamensis*. The results indicate that *B. funiculata* is different genetically from *B. siamensis* (see Figs. 3,4). Enzyme differences between *B. s. siamensis* and *B. s. goniomphalos* were not great. Of the 12 enzymes tested, the two subspecies differed only in EST-1, EST-2 and EST-4. The clear variation of isoenzymes was seen in EST-2 and EST-4 (Figs. 3,4). The results from this study for non-specific esterase activities have indicated genotypic difference between these two snail subspecies; however, further study is required in order to determine whether these snails are separate species. By using only two enzyme systems (PGI and EST), the diagram in Fig. 4 demonstrates a convenient method for accurate identification of these snail species and subspecies.

Attempts to correlate between enzyme types and susceptibility to the parasite have not been very successful and no correlation is found from the present data. Rollinson & Southgate (1979) studied closely related species of *Bulinus* snails. They found that all species had their own specific enzyme types but not correlation could be detected between snail enzyme types and susceptibility of the snails to schistosome parasites. It has been suggested that degree of susceptibility to *Schistosoma mekongi* Voge, Bruckner & Bruce of the alpha, beta and gamma races of *Tricula aperta* (Temcharoen) may be correlated to GOT mobility (Kitikoon, 1982). However, this report is still inconclusive. More studies on other enzyme types and other host-parasite systems may help to confirm or deny this possible correlation.

The value of electrophoretic data must undoubtedly be interpreted with careful studies, since enzyme polymorphisms may also occur within the population. In this study, the wild-caught snails were obtained from various locations in their natural habitats and only the major enzyme loci which were found to show consistent and well-defined bands were taken into account.

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METHOD OF EXPERIMENTAL HYBRIDIZATION AND SOME RESULTS OF ITS APPLICATION IN THE TAXONOMY OF LYMNAEIDAE (GASTROPODA: PULMONATA)

N.D. Kruglov and Y.I. Starobogatov

ABSTRACT

An experimental method of crossing snails for taxonomic purposes is described. This method can be applied to all freshwater pulmonate snails when forms to be compared have genetically determined morphological differences. The method is applied here for a taxonomic study of the species of the lymnaeid subgenus *Lymnaea* s. str. According to their morphology, the large diversity of Palaearctic forms of this subgenus belongs to only six species. These six species also differ in their distributions, and they do not demonstrate intergrades when they live together. These six species are *Lymnaea fragilis, L. stagnalis, L. araratensis, L. doriana, L. media* and *L. bodamica*. There are only five species of this subgenus in the Nearctic: *L. jugularis, L. stagnalis, L. sanctamariae, L. occidentalis* and *L. lepida*.

Experiments on the hybridization of *Lymnaea fragilis* and *L. stagnalis* demonstrate that after crossing in either or both combinations (i.e., in regard to which species is acting female and acting male) either non-viable eggs are produced, or the resulting hybrid offspring always have lost their reproductive capacity and/or exhibit diminished viability. Crossing between these two species is easier when *L. stagnalis* acts as female. A third generation of hybrids has been obtained from this combination of parents. In this cross, the shell shape of *L. fragilis* dominates and the reproductive capacity of the offspring diminishes from generation to generation. In the reciprocal combination, hybrids have shell monstrosities and die before emergence from the egg cluster. Morphological disorders in the reproductive systems of F_1 and F_2 hybrids occur. Our results prove the specific independence of *L. fragilis* and *L. stagnalis*, and indirectly testify in favor of the specific status of the other four Palaearctic species.

INTRODUCTION

The application of the biological species concept in taxonomic practice can be accompanied by some difficulties, because reproductive isolation does not always lead to morphological alterations, and morphological alterations are not always the cause of reproductive isolation. New methods of taxonomy (electrophoretic analysis of proteins, caryology, serological analysis of antigens, etc.) may aid in the study of similarities or differences in populations, but data obtained by these methods may be of limited value in the evaluation of degrees of reproductive isolation. Information on conspecificity or reproductive isolation must be obtained from hybridization experiments.

Experimental hybridization, being connected with the current generally accepted concept of the biological species, can provide precise information on species independence in the case where crossing cannot be achieved (in the absence of external hindrances to it) or where hybrids obtained as a result of it have low reproductive capacity or viability. On the contrary, even if crossing has been successful and hybrids live and reproduce themselves very well, we are not completely sure of species independence, because there are cases where different species after crossing produce viable and fertile hybrids. This one-sided interpretation of the results of experimental hybridization has been discussed previously (Starobogatov, 1977).

Using experimental hybridization, one may prove the species independence of forms not differing or differing little in their morphology. The application of this method in the taxonomy of infusorians has been especially successful (Sonneborn, 1957, 1975). Unfortunately, analysis of the results of crossing two similar forms is possible only when we can obtain clonal

cultures of the animals (the method of preparation of such cultures has been worked out very well for infusorians). Other groups of animals with obligate cross-fertilization may be studied easily by this method, because the fact of reproduction of a female which has not previously been in contact with any male except that which has been introduced to her by the experimenter is evidence that the crossing has taken place and one can further study the properties of hybrids. Such research has given valuable information in the taxonomy of small mammals (Mejer et al., 1973), amphipods (Pinkster, 1972), locusts (Sychev, 1979), and some other groups of animals.

In the course of the taxonomic revision of freshwater pulmonate gastropods and the establishing of new species, the absence of information on their reproductive isolation is felt very sharply. But pulmonate gastropods are very difficult objects for experimental hybridization. Their capacity for self-fertilization leads to difficulty in deciding whether the progeny is the result of self-fertilization or cross-fertilization between different forms. On the other hand, their capacity for self-fertilization enables us to obtain clonal cultures of these animals. However, this process is very time consuming and difficult. In order to differentiate between the results of self- and cross-fertilization, one often can use genetically marked specimens. The simplest method has been used by Paraense (1956), Richards (1973) and Wu (1973) in a series of excellent works on the taxonomy of medically important Planorbidae and Bulinidae. The methodology for such studies has been described in a special article (Paraense, 1956). These authors have used as marked specimens recessive mutants devoid of pigments (among them eye pigment). In this condition, when a pigmentless specimen (red in color due to hemaglobin not being masked by melanin) has laid eggs in which have developed pigmented embryos (with eye-spots), we may conclude that cross-fertilization has taken place. However, in the majority of cases, the authors cited have reported only the success of the cross-fertilization and have not analyzed the properties of hybrids. Meanwhile, such analysis can demonstrate that, in spite of successful cross-fertilization, in some cases the authors dealt with different species. Wu's (1973) experimental work on *Bulinus* is devoid of such deficiency because he has studied the fertility of the F_1 generations. The main difficulty in the application of this method to other groups of pulmonates is that the recessive mutants simply observed by external properties are present only in a few species. Probably such mutants may be found in many species in the course of detailed investigation, but it is very difficult work requiring the study of very large numbers of specimens and genetic analysis of dozens of generations during many decades. One may study the proteins by electrophoretic methods, but these also require difficult preliminary work and, besides, the killing of the specimens being studied is required.

In view of these difficulties, we have worked out a method of experimental hybridization of pulmonates without using genetically marked specimens or, more precisely, using genetically determined features of mollusks found in nature independent of the properties of genetic systems determining the feature. Our method may be regarded as a result of further elaboration of that used by Burch & Ayers (1973) on *Stagnicola elodes* (Say) and *S. emarginata* (Say).

CROSSING EXPERIMENTS

In preparation for the crossing experiments, a good cultivation method has to be devised (in particular, in regard to optimal water volume, quantity and quality of food, temperature, etc.), and a sufficient number of the forms to be compared has to be isolated from the moment of emergence from the egg cluster and until the time of full reproductive capacity. Studying the reproductive biology of the compared forms is also very important. This problem has been discussed previously for Lymnaeidae (e.g., see Horstmann, 1955; Beriozkina et al., 1973; Kruglov & Beriozkina, 1978; Kruglov, 1979a,b, 1980).

A study of conchology, anatomy and egg-cluster structure also is important in preparing for the experiments. It is necessary to find those morphological features by which the hybrids can be precisely differentiated. We know that good results in the identification of close species of Lymnaeidae can be obtained by comparing shell whorls, fine structure of egg clusters, dimensions of egg capsules, and by comparing the

proportions of the copulative organs (using the same methods of fixation for all specimens) (Kruglov et al. (1979); Davydov et al. (1981)).

We use three control aquaria for each experimental aquarium in each series of experiments. A pair of specimens belonging to the two forms to be compared is put in each experimental aquarium. A single specimen of each form is put in control aquarium no. 1. This control aquarium is used for study of mollusk reproduction by self-fertilization. A pair of specimens belonging to the same form is put into control aquarium no. 2 (at least two aquaria). This control aquarium is used for study of normal reproduction of the mollusks by cross-fertilization. The two groups (of three or four specimens) of both species to be compared are put into control aquarium no. 3. This control aquarium is used for the study of selective copulation in the forms studied. All mollusks must be of the same age (the same number of days) in order to exclude the influence of age differences. All mollusks in the experiments must be marked with numbers. This may be done by nitro-staining a dried portion of the shell of the living mollusk. When the stain has dried, the mark is covered by bakelite-phenol glue. Such a marking method enabled us to see the mark during 200-300 days of experiments.

Precise observations must be done on each experimental and control aquarium. Special attention must be paid to duration and type of copulation and to the time of appearance of the first egg clusters. In connection with the discussion on copulation, it is necessary to look at the ethology of copulating mollusks. Lymnaeidae doubtless have selective copulation, i.e., more often copulation is between specimens of the same species when different species are present in the same aquarium. When selective copulation is excluded (by the presence of only two specimens belonging to different species), interspecific copulation is possible. We have seen under laboratory conditions copulation between *Lymnaea palustris* (Müller) and *L. transsylvanica* Kimakowicz, *L. atra* (Schranck) and *L. palustris* (Müller), *L. patula* (da Costa) and *Physastra* sp. (family Bulinidae). In natural water bodies, we may see copulation between *L. stagnalis* (Linnaeus) and *L. fontinalis* (Studer), *L. auricularia* (Linnaeus) and *L. media* Hartmann. Copulation between specimens belonging to different species, different subgenera (as in the latter two cases), and even between different families (as between *Lymnaea* [Lymnaeidae] and *Physastra* [Bulinidae]), demonstrates that the precopulational isolating mechanisms in freshwater pulmonate gastropods are somewhat weak (Kruglov, 1980). This prevents us from drawing a decisive conclusion on the sole fact of the copulation of two specimens belonging to different forms.

After copulation, the mollusks must be isolated in similar aquaria with similar conditions. The most careful registration of the appearance of the first egg clusters of mollusks from experimental and control (no. 1 and no. 2) aquaria is necessary. One must bear in mind that the first egg cluster after self-fertilization appears two to three weeks later than after cross-fertilization (Kruglov, 1980). This peculiarity may be used as additional evidence in the analysis of the fertilization type in mollusks being studied.

The egg clusters obtained are placed individually in Petri dishes for development and appearance of young specimens. After their emergence from the egg cluster, the young mollusks are separated from each other in small aquaria and later in larger aquaria during growth. Special attention must be paid, of course, to specimens appearing from the egg clusters laid after copulation between the two forms being studied.

After the young snail appears, it must be identified as belonging to a particular form by the shape of the embryonic shell. After maturation, the mollusks are analyzed again and their taxonomic position is established. Simultaneously, the reproductive capacity of the mollusks is studied, their fecundity is established, and also, if possible, the fecundity of their progeny. It is also necessary to study the morphology of egg clusters (syncapsules) *in vivo*, especially in specimens appearing after copulation of two forms being compared. It is important to establish precisely the number of egg capsules per syncapsule and presence and percent of defective eggs (e.g., eggs not surrounded by egg capsula). In addition, some specimens regarded as hybrids after they have matured are dissected in order to find any disorder that may have occurred in the reproductive system, especially with the gonads (sometimes the upper part of the visceral sac containing the gonad and the liver, or the whole reproductive system, is fixed in Bouin's liquid for subsequent histological study).

The results of hybridization may give two negative results: 1) the forms studied cannot produce completely fertile progeny, and 2) fertile progeny may be obtained from only one of the mating combinations. Both situations differ genetically and are of equal value from the point of view of species independence, because both situations equally prevent the populations studied from busing into one population, in spite of the absence of any external obstacle (Starobogatov, 1968).

The method described above permits us to analyze the results of the experimental crossing of any two forms found in natural water bodies. As an example of the results of the application of this method, we describe below the study of reproductive isolation of *Lymnaea stagnalis* and *L. fragilis* (Linnaeus).

MORPHOLOGICAL AND ZOOGEOGRAPHICAL DATA ON THE TAXONOMY OF THE *LYMNAEA STAGNALIS*-GROUP

The *Lymnaea stagnalis*-group (i.e., the subgenus *Lymnaea s. str.* of the genus *Lymnaea*) is

regarded from the end of the last century as represented by the single but very variable species *L. stagnalis*. Westerlund (1885) listed 28 infraspecific forms of this species within the Palaearctic region. Baker (1911) also listed many forms of this species within the Nearctic region, although he regarded some of them (e.g., *L. lepida*) as independent species. As a result, the list of synonyms and infraspecific forms contain about 50 nominal species (Hubendick, 1951). The latter author was inclined to regard all American forms as a separate subspecies, *L. s. appressa*, although he discussed no morphological difference of American and Palaearctic forms.

Conchological analysis of the forms of *Lymnaea stagnalis* from water bodies of the U.S.S.R. and Western Europe (using the very rich collection of the Zoological Institute of the Academy of Sciences of the U.S.S.R.) has shown six main forms. In this work, Izzatullaev & Starobogatov's (1984) comparative method is established as the most useful. This method is described briefly as follows. The shell (except the last whorl) is drawn with a camera lucida using a stereoscopic microscope with established magnification (5x or 6x). It is necessary that the axis of the shell coincide precisely with the plane of the picture, but the position of the aperture may be arbitrary. The shell of the form to be compared is put on the table by the microscope (also with the axis parallel to the plane of the picture or to the plane of the table) and is rotated around the axis until one of the whorls (the largest is preferable) coincides with one of the whorls in the picture made by camera lucida with the same magnification. After that, other whorls must be compared without rotation of the shell. It is important to compare the ends of the projections of sutures because the flatness of the whorls may be variable. After studying many species of Gastropoda (both Prosobranchia and Pulmonata), we have established that all whorls (except the last especially near the aperture) of all specimens of the same species coincide precisely in spite of difference in the region and station where the specimens were collected. There are also some exceptions which defy classification: one cannot conclude that coinciding specimens are conspecific and those not coinciding belong to different species. One of the causes of whorls not coinciding is displacement of the whorls along the shell axis. This case is very common in the *L. stagnalis*-group, and it may be established by moving the picture (after the coinciding of one whorl) along the shell axis. The influence of variability of the whorl arising in the magnifications recommended is practically absent; greater magnifications make this influence evident, but smaller magnifications diminish the decisive properties of the method.

Six forms (Fig. 1, a-f) delineated within the *Lymnaea stagnalis*-group differ from each other not only conchologically, but also by their own peculiar distributions, which partly coincide. Although found together, these forms are not connected by a transition and look like a separate species. There are also some differences between them in the structure of their reproductive systems (Fig. 3, a-f) and especially in the proportions of their copulatory structures (Table 1). Biometrical comparison in almost all forms by the index length of preputium/length of penis sheath has allowed us to establish confident difference between almost all forms studied. Such difference has been established not only between *L. stagnalis* and *L. bodamica* Miller and between *L. fragilis* and *L. media*, but the shape of their shells also differs. The data discussed above allow us to suppose that in the Palaearctic region the group of *L. stagnalis* is represented by six species. A list of these species with brief data about distributions and characteristic biotopes follows.

Lymnaea stagnalis (Linnaeus 1758) (Fig. 1a) is distributed from the Atlantic shores to the Kolhyma drainage area inclusively. As a rule, it lives between water plants in permanent, small water bodies.

Lymnaea fragilis (Linnaeus 1758) (Fig. 1b) (synonym: *L. stagnalis* variety *producta* Colbeau 1859) is distributed from the Atlantic shores to the Yenisei drainage area inclusively. It lives between water plants in permanent and semi-permenent water bodies in shallow water; it is more tolerant to drying acidification and mineralization of water than any other species of the subgenus.

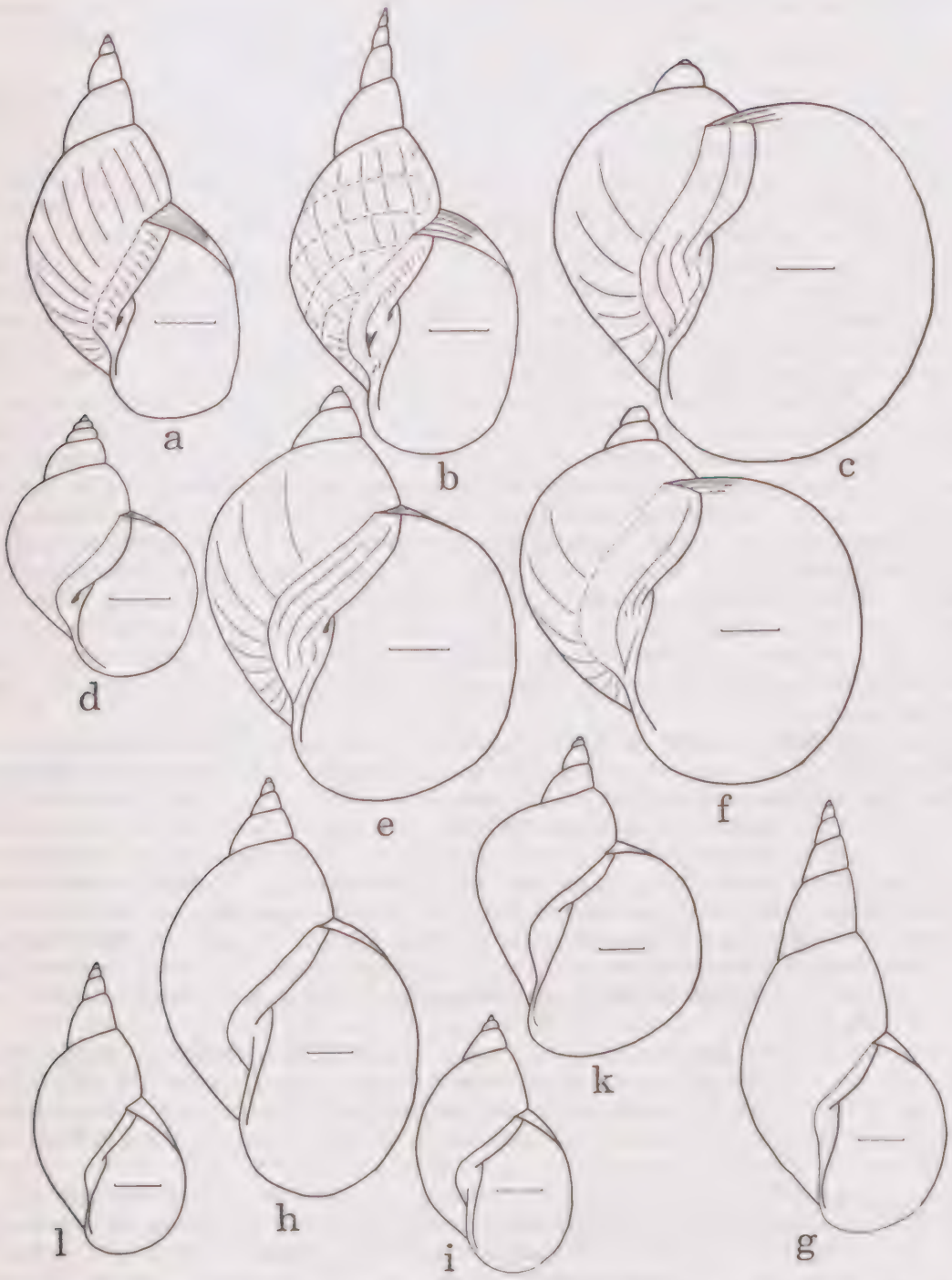

FIG. 1. Shells of the subgenus *Lymnaea s. str.* a-f, Palaearctic species from the U.S.S.R.: a, *L. stagnalis* (Krivoje Lake, Smolensk region); b, *L. fragilis* (Rytoje Lake, Smolensk region); c, *L. bodamica* (Sviatozero Lake, Karelian A.S.S.R.); d, *L. araratensis* (holotype, pond near the railway station Masis, Armenian S.S.R.); e, *L. doriana* (Sviatozero Lake, Karelian S.S.R.); f, *L. media* (from the same locality). g-l, Nearctic species: g, *L. jugularis*; h, *L. stagnalis lillianae* (syntype, after Baker, 1911); i, *L. sanctamariae* (syntype, after Baker, 1911); k, *L. occidentalis* (syntype, after Baker, 1911); l, *L. lepida* (syntype, after Baker, 1911). Scale = 5 mm.

Lymnaea bodamica Miller 1873 (Fig. 1c) is distributed only in Northwestern Europe (Baltic and North seas drainage areas and adjacent regions of Scandinavia, Karelian SSR and Kola Peninsula). It lives in breaker zones of lakes, usually on the stones.

Lymnaea araratensis Kruglov & Starobogatov, sp.n. (Fig. 1d) (syn.: *L. elophila* Kobelt 1877, *non* Bourguignat 1862, *L. omsiana* Hubendick 1951, *non L. homsiana* Locard 1883) is distributed in water bodies of the Mediterranean area. Its distribution is known to include Italy (Kobelt, 1877, pl. 35, fig. 1231), Armenian SSR, Kirghizian SSR (Lake Son-kul) and in the Pamirs (Hubendick, 1951, p. 44, figs. 29, 36). Some reports of *L. stagnalis* var. *turgida* Menke in Asia Minor probably should be referred to this species. The shell is ovate-conical, consisting of six to seven whorls, which increase rapidly, but comparatively evenly, making the tangent line of all whorls (except the last) a straight line (but the last whorl protrudes somewhat through it). The whorls are weakly but evenly inflated and are divided by shallow, moderately inclined sutures. The last whorl is ovate, its height forms 0.7-0.8 of the height of the entire shell and protrudes over the aperture by 0.2-0.3 of the height of the aperture. The last whorl is ovate with an almost straight parieto-palatal angle. The columella is weakly twisted, but nevertheless the columellar fold is somewhat evident. The parietal lip is thin and light, the palatal border sharp. The color and design on the roof of the mantle cavity (light brown and spotty) is poorly visible through the shell. The spire constitutes 0.60-0.61 of the height of the shell. The width of the shell is 1.61 times less than its height. The dimensions of the holotype with six whorls: height of shell, 30.0 mm; width of shell, 19.0 mm; height of spire, 18.5 mm; height of aperture, 18.0 mm, width of aperture (without columellar flap, 11.0 mm, width of aperture (with columellar flap), 13.0 mm; height of last whorl, 24.0 mm; width of last whorl (without aperture), 13.2 mm. The holotype was collected in Armenian SSR in the pond near the railway station Masis. It is deposited in the collection of the Zoological Institute of the Academy of Science of the U.S.S.R., and is listed as no. 1 in the taxonomic catalogue.

The albumen gland is narrow and strongly elongated, somewhat smaller than the labyrinth of the oviduct. The nidamental gland is large and almost spherical. The uterus is large and divided into distal and proximal parts. The provagina is relatively short and wide, evidently separated from the uterus. The spermathecal duct is somewhat dilated near the vagina. Its reservoir is oval or spherical, with its greater diameter 2.2 times less than the length of its duct. The prostate gland is long, its proximal part band-shaped and somewhat narrowed to the labyrinth, its distal part is pear-shaped. The prostatic duct begins almost terminally. The preputium is massive, slightly narrowed near the male aperture and near the penis sheath. The penis sheath is dilated in the region of the proximal camerae and noticeably narrowed to the preputium. The ratio of the length of the preputium to the length of the penis sheath is approximately 4.

Lymnaea doriana Bourguignat 1862 (Fig. 1e) is distributed in Western Europe (from the extreme North to the Mediterranean area), in Northwestern regions of the U.S.S.R. (Kola Peninsula, Karelian SSR, Baltic region). In the southern part of the U.S.S.R., this species is distributed farther eastward, to the Altai Mountains. It lives in breaker zones of lakes on sparse submerged plants.

Lymnaea media Hartmann 1844 (Fig. 1f) (syn.: *L. stagnalis* var. *lacustris* "Studer" Hartmann 1844) is distributed only in Northwestern Europe (Baltic and North seas drainage areas and adjacent regions of Scandinavia, Karelian SSR and Kola Peninsula). It lives in the littoral zone of lakes on stones and muddy ground.

American malacologists doubtless are interested in how many species are represented in the *Lymnaea stagnalis*-group in the Nearctic region. We cannot discuss this problem decisively, since we have no adequate material (except *L. jugularis* Say). However, after analyzing numerous data on dimensions and photographs presented by Baker (1911), we suppose that the group in question is represented in the Nearctic region by five somewhat different forms.

TABLE 1. Ratios of shell height/width and preputium length/penis sheath length for six species of *Lymnaea*.

Species	No. of specimens dissected	Ratio of shell height/width	Ratio of preputium length/penis sheath length
L. stagnalis	50	1.94 ± 0.06	3.08 ± 0.21
L. fragilis	50	2.38 ± 0.18	4.37 ± 0.31
L. bodamica	10	1.28 ± 0.04	3.30 ± 0.13
L. media	10	1.38 ± 0.09	5.75 ± 0.69
L. doriana	10	1.46 ± 0.07	4.07 ± 0.17
L. araratensis	1	1.61	4.00

These are discussed below.

Lymnaea jugularis Say 1817 (Fig. 1g) (syn.: *Lymnaeus appressus* Say 1818) is distributed in North America eastward from the main American watershed and northward from the parallel 40° N latitude. It lives in overgrown parts of permanent water bodies.

Lymnaea stagnalis (Linnaeus 1758) (Fig. 1h) (known in America under the names *L. stagnalis perampla* Walker 1908 and *L. stagnalis lillianae* Baker 1910) is distributed only in the Great Lakes region, where undoubtedly it has been introduced from Europe. It lives in the same biotopes as in Europe.

Lymnaea sanctamariae Walker 1892 (Fig. 1i) is distributed in the eastern part of North America from the Great Lakes region to the shore of the Gulf of Mexico. It lives in the breaker zones of lakes on stones and muddy ground.

Lymnaea occidentalis Hemphill 1890 (Fig. 1k) is distributed westward from the main American watershed and lives in lakes.

Lymnaea lepida Gould 1847 (Fig. 1l) (syn.: *L. stagnalis wasatchensis* Baker 1911) is distributed westward from the main American watershed and lives in permanent water bodies on plants.

We have not undertaken the task of revising the taxonomy of American forms of the group in question because we have no adequate original material. In spite of this, it is necessary to underline that all American forms (except *Lymnaea stagnalis*) differ appreciably from European forms. It is very probable that independent species must have appeared in America because the representatives of the subgenus are known on this continent from the mid-Miocene (*L. mascallica* Cossmann 1907, syn.: *L. staernsi* Hannibal (in Baker) 1911, is similar to the Palearctic *L. araratensis*, but is larger).

We must discuss the morphological difference between *Lymnaea stagnalis* and *L. fragilis* in more detail, because we have used these species (as the most widely distributed, variable and the simplest for cultivation) for crossing experiments. The data presented here are based on natural populations from which the materials for experiments have been obtained: namely, *L. fragilis* from Rytoye Lake and *L. stagnalis* from Krivoye Lake. Both lakes are located in the Smolensk region, U.S.S.R. The distance between the localities of the two populations is about 80 km. However, this distance cannot explain the low fertility of the hybrids, because our previous experiments on either *L. stagnalis* or *L. fragilis*, obtained from localities which are hundreds or thousands of kilometers apart (Karelian ASSR, Smolensk and Astrakhan regions), produced abundant, viable and fertile progeny.

The shell of adult *Lymnaea fragilis* (i.e., with a height of 53.2 ± 2.0 mm) is slender with a needle-like spire and flat whorls. The height of the spire is not less than the height of the aperture, but in general it is 1.5-2 times more than the latter. The last whorl constitutes 0.67-0.72 of the shell height, and the ratio of shell height to shell width (for 50 specimens) is 2.38 ± 0.08.

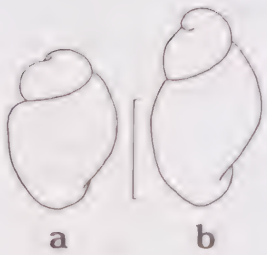

FIG. 2. Embryonic shells of (a) *Lymnaea stagnalis* and (b) *L. fragilis*; age = one day. Scale = 1 mm.

The shell of adult *Lymnaea stagnalis* (i.e., with a height of 43.9 ± 0.9 mm) is less slender with a high conical spire and weakly inflated whorls. The height of the spire is always less than the height of the aperture. The last whorl constitutes 0.75-0.80 of the shell height and the ratio of the shell height to shell width (for 50 specimens) is 1.94 ± 0.06. It is evident that the ratios mentioned above differ with confidence (td = 4.4; $P < 0.001$) from each other.

The difference in shell structure may be seen immediately after emergence of young specimens from the egg cluster. Specimens of *Lymnaea stagnalis* have an almost spherical shell with weakly inclined sutures (Fig. 2a). Conversely, specimens of *L. fragilis* with the same number of whorls are more elongate and their sutures are perceptibly inclined (Fig. 2b).

There are also some differences in the structure of the reproductive system (Fig. 3). These differences are mainly in the proportions of the copulatory organs. The ratio of the preputium length to penis sheath length in *Lymnaea fragilis* (in 50 specimens) is 4.37 ± 0.31, but in *L. stagnalis* this ratio (in 50 specimens) is 3.0 ± 0.21. It is evident that statistically these ratios differ significantly (td = 3.5; $P < 0.001$). In addition, *L. stagnalis* has a shorter prostate gland than *L. fragilis* and the prostate gland of the former is widened to the quadrivium (carrefour), but not widened in the latter species. The spermathecal duct is widened near the mouth in *L. stagnalis* and not widened in *L. fragilis*.

Differences between the two species also are found in the structure of syncapsules[1], i.e., egg clusters (Fig. 4). In the syncapsules of *Lymnaea fragilis*, the egg capsules are arranged in two rows, but in the syncapsules of *L. stagnalis* the egg capsules (with the same number) are arranged in three or four rows. In addition, the egg capsules of *L. fragilis* are more elongate

TABLE 2. Differences between *Lymnaea stagnalis* and *L. fragilis* in syncapsules and egg capsules.

Character	*L. stagnalis*	*L. fragilis*
No. of egg capsules/syncapsule	43.0 ±4.5	49.6 ±1.6
Length of syncapsule (mm)	20.7 ±1.9	18.3 ±1.6
Width of syncapsule (mm)	4.2 ±0.1	4.2 ±0.5
Length of egg capsule (mm)	1.33 ±0.003	1.52 ±0.01
Width of egg capsule (mm)	0.94 ±0.003	1.01 ±0.01

[1] Terminology after Beriozkina & Starobogatov (1981). In the literature, the syncapsule is commonly named "egg capsule", the egg capsule "egg", and the intercapsular string partly "egg string", partly "capsular string". The emendation is to unify the terminology for the Pulmonata and for the majority of the Prosobranchia (e.g., the egg cluster in the Valvatidae and the Lymnaeidae is a syncapsule, but in the remaining oviparous Prosobranchia it is an egg capsule).

FIG. 3. Reproductive systems of Palaearctic species of the subgenus *Lymnaea s.str.* a, *L. stagnalis*; b, *L. fragilis*; c, *L. bodamica*; d, *L. araratensis* (holotype); e, *L. doriana*; f, *L. media*.
ag = albumen gland; lov = labyrinth of oviduct; ng = nidamental gland; pp = preputium; pr = prostate gland; ps = penis sheath; pv = provagina; sr = spermatheca; srd = spermathecal duct; sv = seminal vesicles; ut = uterus; vd = vas deferens. Scale = 2 mm.

than those of *L. stagnalis*. They differ with confidence from each other by the ratio of length of the egg capsule to its width (td = 10; $P < 0.001$). The egg capsules of *L. fragilis* have a stronger external lamellar envelope, and more strongly developed inter-capsular strings, which sometimes form a partition-like pattern. Quantitative differences between egg capsules of *L. stagnalis* and *L. fragilis* (in 30 syncapsules for each species) are presented in Table 2.

It can be seen that the differences between the compared forms are not great, but they are sufficiently clear and are present not only in the shell (including its embryonic part) but also in the reproductive system and syncapsule. We must state also that all features listed have been constant during the cultivation of some generations.

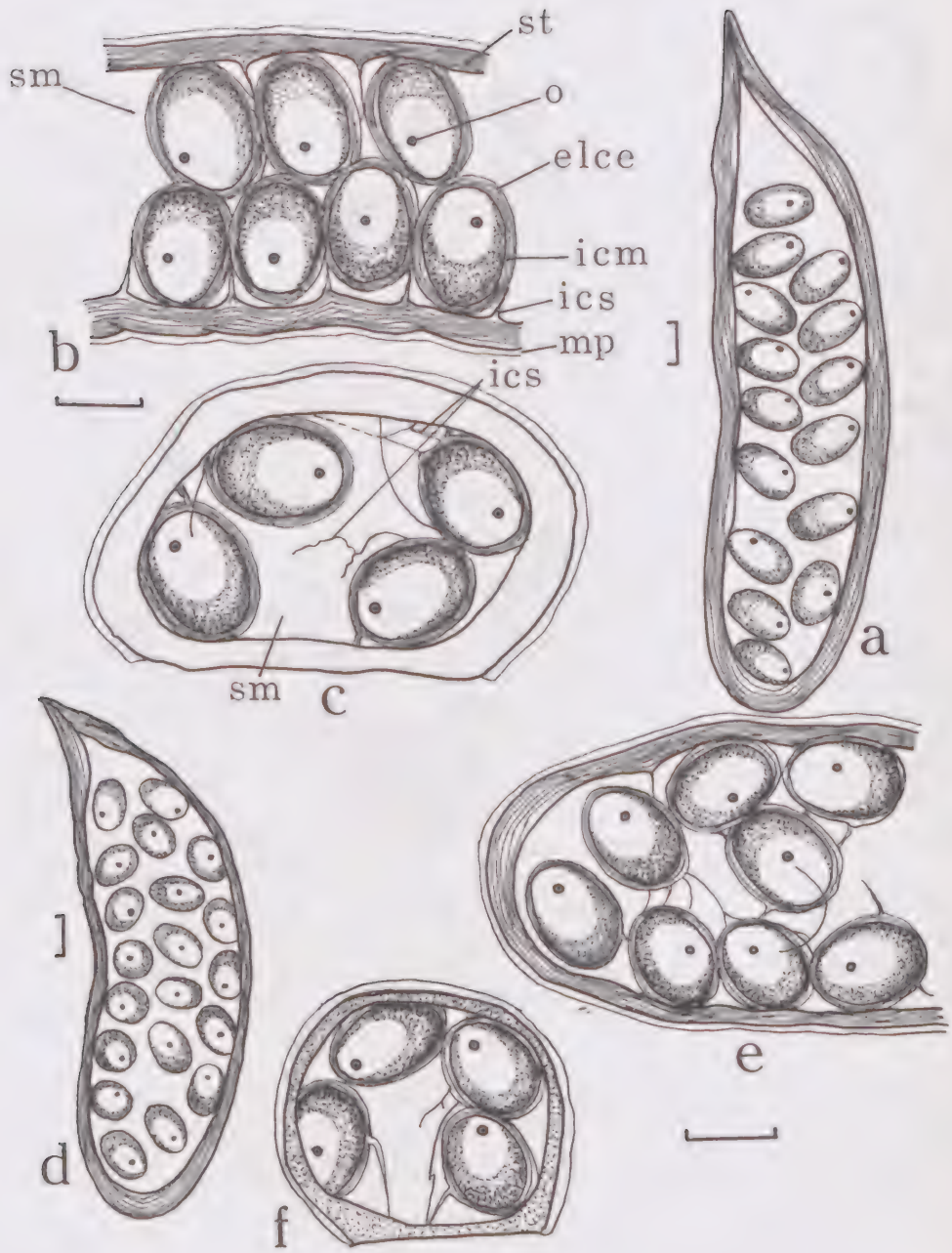

FIG. 4. Syncapsules of *Lymnaea fragilis* (a-c) and *L. stagnalis* (d-f). a, d, View from above; b, e, fragment of the syncapsule magnified (intercapsular strings are visible); c, f, transverse section through the syncapsule.

elce = external lamellar capsular envelope; icm = internal capsular membrane; ics = intercapsular strings; mp = mucous part of syncapsular envelope; o = egg (embryo); sm = syncapsular matrix; st = syncapsular envelope. Scale = 1 mm.

RESULTS OF EXPERIMENTAL CROSSING

Snail specimens of one precise age (in days) raised in culture were used for our experiments. A water volume of 500-1000 ml per specimen and a temperature of 20-22°C was

found to be optimal for growth and development of the snails. Well-macerated leaves of poplar, lettuce and cabbage, as well as leaves of *Vallisneria spiralis* Linnaeus, were used for food. The syncapsules obtained were transferred to Petri dishes for development at the same temperature. Development requires 12-14 days. Specimens of the different forms copulated with each other (which occurred in the experimental aquaria and control aquaria no. 3 of all series of experiments), as males by *Lymnaea stagnalis* in some cases, as *L. fragilis* in others. The period of such copulations coincided with the maximum number of anomalies in the syncapsule structures (about 30% of the syncapsules). The anomalies were varied: some had embryos without capsular envelopes, some egg capsules were without embryos, and in some cases there were sharp deviations in the shape and dimensions of the egg capsules. In particular, in one of the experimental series in which *L. stagnalis* acted as a female, a syncapsule was obtained (12 Jan. 1978) containing 13 egg capsules devoid of embryos. Another syncapsule in the same experimental series contained 37 egg capsules, 26 (71%) of which had no embryos. From 11 egg capsules remaining after 12 days, 11 specimens appeared which completely agreed with *L. stagnalis* in shape. Later, their identity with *L. stagnalis* was proven by morphological studies, which leads us to conclude that these 11 egg capsules had been fertilized by autosperm and the death of the remaining ones was connected with their fertilization by allosperm (Fig. 6).

In some cases, mixed progeny appeared from the syncapsules laid by *Lymnaea stagnalis* after copulation with *L. fragilis*: specimens with the lower spire characteristic for *L. stagnalis* and the higher spire characteristic for *L. fragilis* (Fig. 5a-d). The former, as has been demonstrated by subsequent morphological analysis, do not differ from the mother specimen and probably developed from self-fertilized eggs, but the latter doubtless were hybrids, and we must regard the height of their spire as a dominant feature.

It may be suspected that, from the syncapsules laid by *Lymnaea fragilis* after copulation with *L. stagnalis*, uniform progeny will appear with the high spire characteristic for this form. But, instead, a different result was obtained: from syncapsules laid by *L. fragilis* after copulation with *L. stagnalis*, specimens of two types appeared – some completely agreed with young *L. fragilis* and others had a really monstrous shell, the monstrosity being connected with transformation of the coiling of the shell spire (Fig. 5e-k). It is very probable that the former developed from self-fertilized eggs, but the monstrosities were the result of cross-fertilization by the allosperm.

Further results of our crossing experiments will be discussed separately for two combinations: (1) when *Lymnaea stagnalis* is the female, and (2) when *L. fragilis* is the female.

(1) *Lymnaea stagnalis* as a female (Fig. 5a-d). The majority of syncapsules laid in the experiments by *L. stagnalis* after copulation with *L. fragilis* contained self-fertilized eggs and some nonviable eggs. Only 12-13% of the syncapsules contained specimens with two types of shells (i.e., contained some hybrids). However, the percentage of hybrids, in general, was lower (6-7% of the number of progeny). All syncapsules obtained as a result of cross-fertilization between two *L. stagnalis* under the same conditions had no anomalies and after 12-14 days the progeny had hatched from almost all egg capsules.

In order to study the fertility of hybrids, they (and also *Lymnaea stagnalis* from self-fertilized eggs) were cultivated for obtaining their progeny. *L. stagnalis* developed from self-fertilized eggs began egg laying at age 95-100 days. Their syncapsules had no visible anomalies and only *L. stagnalis* hatched from them. The hybrid specimens (15 in number) laid the first syncapsule at age 110 days. During the period 8 Dec. 1977-28 Nov. 1978, 255 syncapsules were obtained from the hybrids; of these, 85 syncapsules were cultivated in order to study development. Development of the embryos was stopped in the egg-cleavage stage in 59 (70%) of the syncapsules; after that the embryos died and dissolved. All syncapsules in which the embryos could not develop normally had serious anomalies (Fig. 6).

Dissection of adult F_1 hybrids demonstrated that all parts of their reproductive systems were well developed. However, the evident anomaly was present in the gonads. The central part of the gonad was distorted by connective tissue. The inherent ruptures of the gonadial duct from which the oocytes fall out were present in some parts.

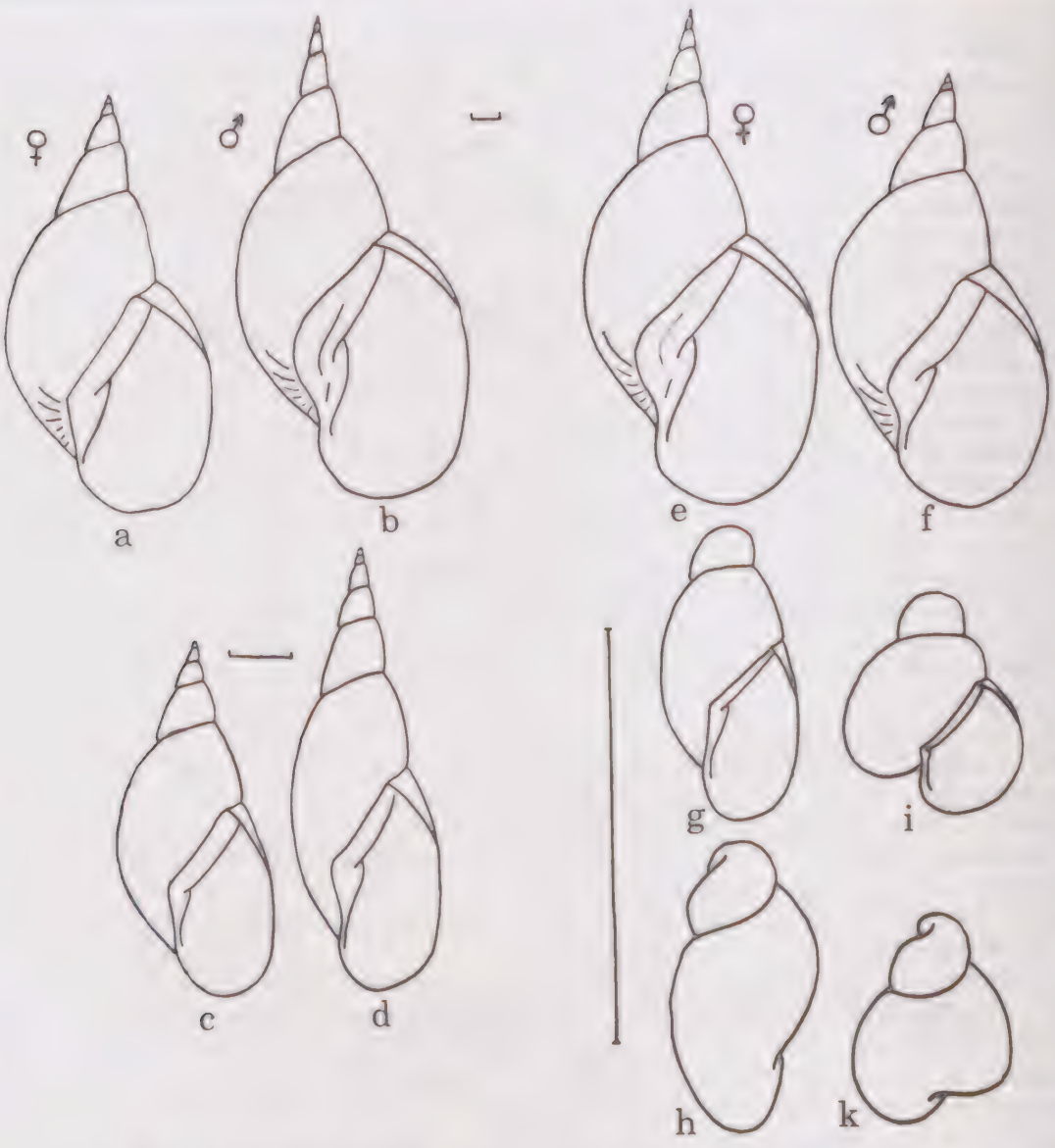

FIG. 5. Results of crossing *Lymnaea stagnalis* and *L. fragilis*. a, *L. stagnalis* (female); b, *L. fragilis* (male); c, d, progeny from the same syncapsule; c, result of self-fertilization; d, result of cross-fertilization (i.e., a hybrid); e, *L. fragilis* (female); f, *L. stagnalis* (male); g-k, progeny from the same syncapsule; g, h, results of self-fertilization; i, k, results of cross-fertilization (hybrids died before emergence from syncapsule). Scale = 3 mm.

Eight F_2 hybrids developed to the adult stage and laid the first syncapsule at age 142 days. Until age 218 days, these eight specimens laid 22 syncapsules containing all together 541 egg capsules (average: 24.5 egg capsules per syncapsule). These syncapsules also had serious anomalies (Fig. 6e). From 10 syncapsules cultivated for development (Table 3), in seven the embryos died and in three some egg capsules had snails which developed but had a high death rate of progeny. In addition, it must be stated that the F_2 hybrids usually died after egg laying.

The dissection of one F_2 hybrid specimen demonstrated that the germinative epithelium of the gonad was substituted in some parts by connective tissue. The uterus had a shape uncommon for both *Lymnaea stagnalis* and *L. fragilis*: it was strongly elongated, irregular in form and passed smoothly to the provagina (Fig. 6a-c). The latter was very short and wide,

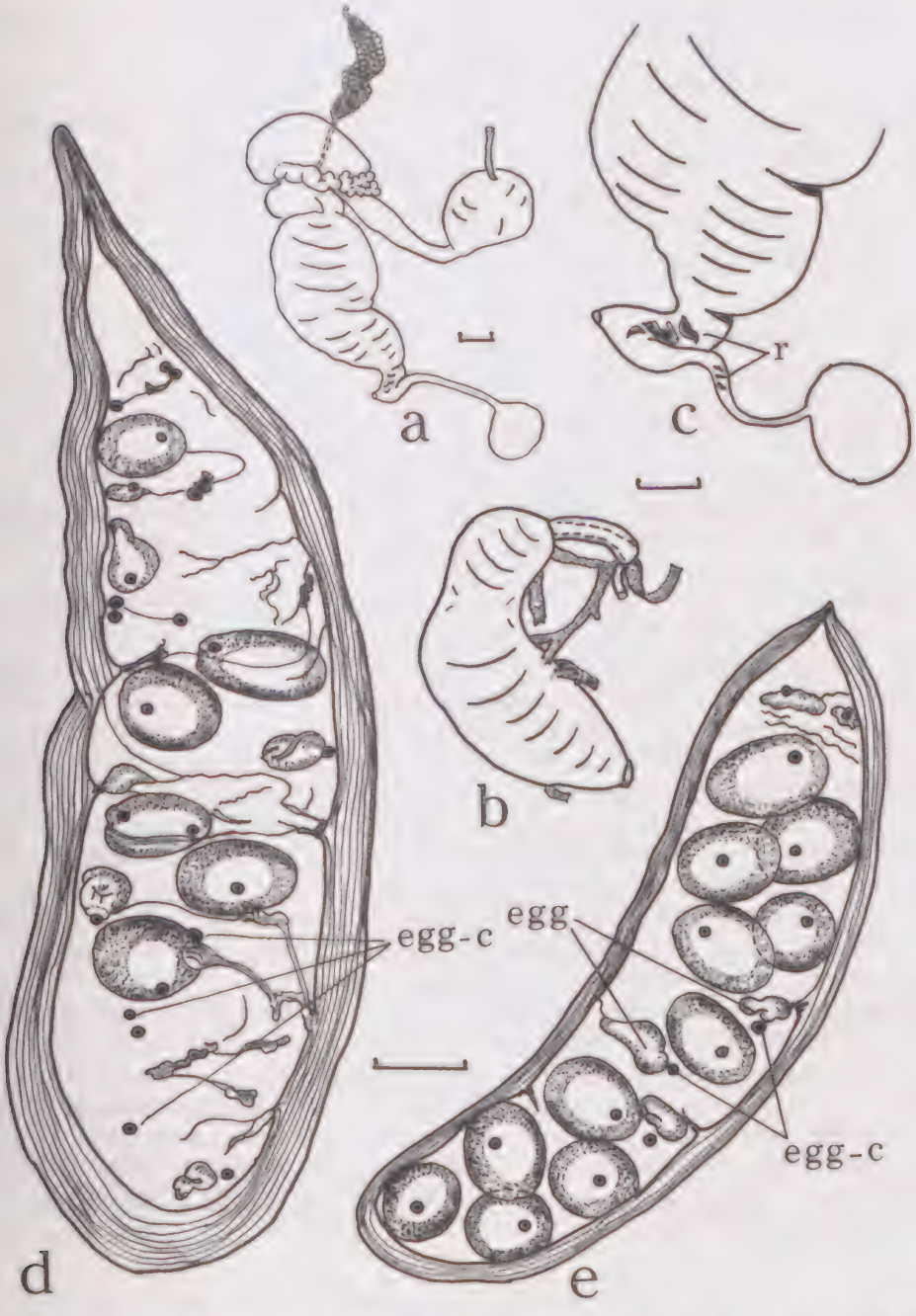

FIG. 6. Anomalies in the structure of genitalia and syncapsules of hybrids. a-c, Genitalia of F_2 hybrids. a, Reproductive system (general view) without gonad and copulatory apparatus; b, copulatory apparatus; c, fragment of distal part of female division (r = ruptures in provagina and spermathecal duct; see Fig. 3 for explanation of remaining letters). d, e, Syncapsules of F_1 and F_2 hybrids. d, Syncapsule of F_1 hybrid; e, syncapsule of F_2 hybrid. Eggs and embryos (egg-c) without albuminous envelope and egg capsules, and deformed egg capsules (egg), are readily visible. Both syncapsules died during development. Scale = 1 mm.

and was practically devoid of musculature. It is probable that in this case the provagina would rupture, resulting in the death of the mollusk. The spermathecal duct, similar to that found for the provagina, was devoid of muscular and epithelial lining.

TABLE 3. Peculiarity of development of the syncapsules of hybrids (F_1 and F_2) and cross-fertilized *Lymnaea stagnalis* and *L. fragilis*.

Forms	No. of syncapsules in development study	Syncapsules with dead embryos (%)	No. of egg capsules in development study	Appearance of progeny (%)
F_1 hybrids	85	70	2022	26.7
F_2 hybrids	10	70	266	35.7
Cross-fertilized				
L. stagnalis	14	0	196	94.05
L. fragilis	16	0	207	96.02

From 81 F_3 specimens, we could maintain only three alive. Two of these died at age 5.5 months, and the sole surviving specimen at age 220 days produced the first syncapsule. During the 264 days of life of this specimen, 15 syncapsules containing 81 egg capsules (average 5.4 egg capsules per syncapsule) were obtained.

It is important to note that from syncapsules laid by F_1 and F_2 hybrids, progeny appeared with both relative short spires and relative high spires. The high mortality during the development of the eggs prevented a calculation of the relation of two forms in one syncapsule and consequently the determination of the inheritance of characters in F_2 and F_3 hybrids.

(2) *Lymnaea fragilis* as a female (Fig. 5e-k). As in the previous case among the syncapsules laid by *L. fragilis* after copulation with *L. stagnalis*, the syncapsules with self-fertilized eggs and with nonviable eggs dominated. There were only nine syncapsules in which monsters developed. In some of them, only specimens with abnormal shells (i.e., in the hybrids) developed; in others, there were specimens with normal shells for *L. fragilis* (results of self-fertilization, which is evident because the latter specimens do not differ in either viability or fertility from the progeny obtained from *L. fragilis* in control aquarium no. 2). The majority of the hybrid specimens died before emergence from the syncapsules or some time after that, and we could not maintain the hybrid specimens to adult stage.

The results of the experiments described above prove that hybridization of *Lymnaea stagnalis* and *L. fragilis* in any combination leads to nonviable progeny or to the appearance of progeny with destroyed reproductive capacity and low viability. Crossing was easy when *L. stagnalis* acted as a female. In this case, we were able to obtain third generation hybrids. In addition, in this case the domination of the shell shape characteristic for *L. fragilis* was evident. All results described indicate that *L. stagnalis* and *L. fragilis* are different species. This, in turn, indirectly proves our supposition that there are six species of the subgenus *Lymnaea s. str.* in the Palaearctic realm.

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CORRÉLATIONS ENTRE LA PRÉSENCE DU MOLLUSQUE *BIOMPHALARIA GLABRATA* ET QUELQUES PARAMÈTRES DU MILIEU DANS LES MARES DE LA GRANDE TERRE DE GUADELOUPE (ANTILLES FRANÇAISES)

Jean-Pierre Pointier, André Théron et Florent de Vathaire

RÉSUMÉ

Cent quatre-vingt-huit mares ont été prospectées en Grande Terre de Guadeloupe en 1980-81. De ces mares, 26.6% hébergent *Biomphalaria glabrata*, Mollusque hôte intermédiaire de la schistosomose intestinale dans cette île. Vingt-deux variables ont été étudiées dans ces mares dont neuf concernent la flore et 10 la faune. L'analyse de ces variables par différentes méthodes a montré que la présence de *B. glabrata* en fonction des paramètres du milieu, pouvait être interprétée en relation avec les deux grandes régions de la Grande Terre: les Grands Fonds et le secteur Est et Nord. Dans les Grands Fonds, la présence de *B. glabrata* apparait directement liée à certaines plantes comme les Nymphéacées et les *Pistia stratiotes*. D'autre part, on peut considérer que les Graminées et les Nymphéacées constituent d'excellents indicateurs de la présence de *B. glabrata* que l'on trouve souvent associé au Mollusque *Drepanotrema depressissimum*. Pour la région Est et Nord, les résultats apparaissent plus difficilement interprétables car les variables choisies sont peu explicatives de la présence-absence de *B. glabrata*. Huit espèces de Trématodes parasites de *B. glabrata* ont été trouvés dans les mares de Grande Terre. Leur présence contraste de manière frappante avec l'absence de *Schistosoma mansoni* de ces gites.

ABSTRACT

During the year 1980-81, 188 ponds of Grande Terre, Guadeloupe, were surveyed. Of these ponds, 26.6% harbored *Biomphalaria glabrata*, the intermediate host snail of intestinal schistosomiasis on the island. Twenty-two variables were studied in these ponds, nine of which concerned the flora and 10 concerned the fauna. On Grand Fonds, the presence of *B. glabrata* appeared to be directly linked to that of certain plants, such as the Nymphaea and *Pistia stratiotes*. In regard to the northern and eastern regions, the results obtained appear more difficult to interpret, since the variables selected are little explicative of the absence or presence of *B. glabrata*. Eight species of trematode parasites of *B. glabrata* were discovered in the ponds of Grande Terre. Their presence contrasts strikingly with the absence of *Schistosoma mansoni* in these sites.

INTRODUCTION

Des études réalisées de 1972 à 1978 ont montré que l'aire de transmission de la schistosomose intestinale en Guadeloupe ne se superpose pas à l'aire de répartition du Mollusque hôte intermédiaire *Biomphalaria glabrata*. L'étude des sites de transmission de la maladie a démontré que les foyers les plus actifs étaient répartis dans l'île de Basse Terre: canaux d'irrigation, ravines et site exceptionnel du Grand Etang (Pointier et al., 1977; Rioux et al., 1977; Théron et al., 1977, 1978; Pointier, 1979; Golvan et al., 1981). En revanche, dans l'île de Grande Terre, les sites de transmission apparaissent strictement limités à une étroite zone correspondant aux marécages d'arrière mangrove (Pointier & Théron, 1979). Par ailleurs, les très nombreuses mares et étangs de cette région semblent indemnes de toute contamination malgré la présence du Mollusque hôte intermédiaire.

Une étude des facteurs écologiques responsables de cette situation a été enterprise en 1980-81 afin d'évaluer les potentialités de transmission de la schistosomose dans ces mares et étangs. Dans ce but, deux voies principales de recherches ont été suivies: 1) une prospection intensive des collections d'eau de la Grande Terre afin de préciser la répartition et l'écologie du Mollusque hôte intermédiaire *Biomphalaria glabrata*, ainsi que l'inventaire de la faune parasitologique hébergée par ce Mollusque; 2) une étude des potentialités de développement de *Schistosoma mansoni* dans une mare expérimentale située dans l'Est de la Grande Terre près de Saint-François. Cette étude a été complétée par différentes expériences de laboratoire. Nous présentons dans cet article les résultats obtenus sur l'écologie du *B. glabrata*.

LA GRANDE TERRE DE GUADELOUPE: PRESENTATION SOMMAIRE

La Grande Terre, qui couvre une superficie de 585 km^2, est une île plate, sèche et calcaire. En dehors de la zone côtière qui borde le Grand-Cul-de-Sac-Marin et qui est recouverte par des mangroves et des forêts marécageuses à *Pterocarpus*, deux régions principales ont été distinguées: les plateaux de l'Est et du Nord et les Grands Fonds.

L'Est et le Nord

Il s'agit de la région la plus sèche de la Grande Terre. La pluviométrie annuelle moyenne y est de l'ordre de 1,000 à 1,500 mm. Les reliefs sont faibles et ne dépassent pas 40 à 50 m d'altitude. Les collections d'eau sont représentées par des mares pour la plupart temporaires, naturelles ou artificielles. D'autre part, cette région est traversée, d'Est en Ouest, par un petit cours d'eau, la ravine des Coudes. Cette ravine ne coule qu'en période de crues et le reste de l'année ne présente qu'une succession de petites mares dont beaucoup s'assèchent totalement en été.

Les Grands Fonds

Cette région particulière, très bien décrite par Lasserre (1961), présente un relief tourmenté, alternant dépressions et collines arrondies dont les plus hautes culminent à 135 m. La pluviométrie y est plus importante (1,500 à 2,000 mm) et de très nombreuses mares sont présentes dans le fond des dépressions. Toutes ces mares voient leur niveau baisser en saison sèche et certaines peuvent même s'assècher totalement en été; ces mares temporaires sont toutefois beaucoup plus rares que dans la région Est et Nord.

En ce qui concerne le processus de formation de ces mares et leur évolution, on se reportera aux descriptions effectuées par Jeremie & Raynal-Roques (1978, 1981).

METHODES D'ETUDE DES MARES ET ETANGS DE LA GRANDE TERRE

D'aprés la carte IGN au 1/20,000, on peut estimer à 682 le nombre total des mares et étangs présents en Grande Terre. Ces mares se répartissent de façon inégale entre les Grands Fonds (198) et la zone Est et Nord (484). Cependant, leur densité y est à peu près identique, l'Est et le Nord couvrant une superficie double de celle des Grands Fonds. Des efforts similaires de prospection ont donc été apportés à l'ensemble des régions considérées (Tableau 1). Au total, 188 mares ont été prospectées dont 68 dans les Grands Fonds et 120 dans l'Est et le Nord. Dans chaque mare, différents paramètres ont été analysés à quatre périodes différentes au cours d'un cycle annuel (en juillet 1980, novembre 1980, janvier 1981 et juin 1981).

Les 22 variables qui ont ainsi été considérées comprennent, outre la date des observations, le diamètre de la mare, la conductivité des eaux, des données sur la flore exprimées en pourcentage de recouvrement (nos. 4-12) et des données sur la faune exprimées en terme de présence-absence (nos. 13-22). Ces 22 variables sont les suivantes: 1, date; 2, diamètre; 3, conductivité; 4, Nymphéacées; 5, Graminées; 6, Polygonacées; 7, Characées; 8, Cypéracées; 9, *Pistia stratiotes*; 10, *Ipomea palustris*; 11, recouvrement végétal total; 12, couverture d'arbres; 13, *Poecilia reticulata*; 14, *Tilapia mossambica*; 15, *Biomphalaria glabrata*; 16, *Ampullaria glauca*; 17, *Physa marmorata*; 18, *B. schrammi*; 19, *Drepanotrema lucidum*; 20, *D. depressissimum*; 21, *D. anatinum*; 22, *Potamopyrgus parvulus*.

Une attention particulière a été apportée aux Mollusques et en particulier à *Biomphalaria glabrata*: ¼ à ¾ heure de récoltes ont été effectués dans chaque mare selon ses dimensions, par le même opérateur.

Les Mollusques ont été mesurés et testés au laboratoire quant à l'émission éventuelle de cercaires. Un total de 17,730 *B. glabrata* a ainsi été récolté au cours des quatre périodes d'échantillonnage.

L'analyse des variables a consisté à comparer deux groupes de mares: celles hébergeant *Biomphalaria glabrata* et celles ne l'hébergeant pas. Il s'agit d'étudier quelles sont les variables différentiant le mieux les deux groupes de mares. Pour répondre à cette question, nous avons effectué des analyses classiques et des analyses multivariates.

Les analyses classiques

L'étude de la relation entre la présence de *Biomphalaria glabrata* et celle d'une autre espèce animale revient à faire une comparaison de deux pourcentages observés: le pourcentage moyen de mares hébergeant cette autre espèce animale parmi celles hébergeant *B. glabrata* par rapport à ce même pourcentage moyen parmi celles n'hébergeant pas *B. glabrata*. Il faut donc employer un test de X^2 d'indépendance (Schwartz, 1963) qui offre l'avantage de ne pas supposer la normalité de la distribution du pourcentage dans l'un ou l'autre des deux groupes.

L'étude de la relation entre la présence de *Biomphalaria glabrata* et le pourcentage de recouvrement d'une espèce végétale donnée revient à comparer deux moyennes: le pourcentage moyen de recouvrement dans les mares hébergeant *B. glabrata* par rapport à ce pourcentage moyen dans celles ne l'hébergeant pas. Une telle comparaison est généralement effectuée à l'aide d'un test t de Student. Cependant ce test suppose la normalité de la distribution de la variable étudiée dans chacun des deux groupes à comparer (Schwartz, 1963). La distribution des pourcentages de recouvrement des mares par les espèces végétales n'est jamais ici normale ou proche de la normale. Pour toutes les espèces, ceci est du au fait que le pourcentage de recouvrement est nul dans une très forte proportion de mares. Il serait donc très contestable d'utiliser ce test malgré la taille des échantillons dont nous disposons. Les tests non paramétriques classiques autres que le test de X^2 ne sont pas utilisables non plus car ils consistent à classer des valeurs, et nous aurions ici, toujours pour la même raison citée plus haut, une très grande proportion d'ex-aequo. Pour résoudre ce problème, nous avons choisi de ne retenir que l'absence ou la présence d'un facteur "espèces végétales" et d'effectuer des tests de X^2 d'indépendance. Le principal problème consiste à déterminer à partir de quel pourcentage de recouvrement on doit considérer que le facteur est présent. La prise en compte de l'absence ou de la présence de l'espèce végétale n'est peut être pas suffisante. En effet, il est tout à fait possible que certaines espèces végétales n'aient d'influence que lorsqu'elles recouvrent plus d'une certaine proportion d'une mare donnée. Nous avons donc effectué plusiers tests de X^2 pour chaque espèce végétale en faisant varier la limite en dessous de laquelle l'existence de l'espèce est prise en compte.

L'étude de la relation entre la présence de *Biomphalaria glabrata* d'une part, et la date de prélèvement, le diamètre de la mare et la conductivité de l'eau d'autre part, peut être effectuée à l'aide d'un test t de Student car le problème d'un grand nombre de zéros ne se pose pas avec ces variables.

Analyse multivariates

Nous avons effectué une analyse discriminante linéaire (BMDP Statistical Software, 1981), qui est équivalente dans le cas d'une variable dépendante oui/non à une régression linéaire multiple, afin de déterminer les variables directement liées à la présence de *Biomphalaria glabrata*.

Pour cette analyse nous avons gardé la transformation en variables présence/absence des pourcentages de recouvrement des espèces végétales. Ce choix a été fait parce que nous ne pouvions pas tester les coefficients de corrélations partielles qui supposent la normalité de la distribution des variables dans les deux groupes. Il était alors nécessaire de n'étudier que les coefficients de régression, et donc préférable d'exprimer toutes les variables dans la même unité (présence/absence).

RESULTATS ET DISCUSSION

Sur un total de 188 mares prospectées, 50 hébergent *Biomphalaria glabrata*, soit 26.6% (Fig. 1). Une analyse sommaire de ces données montre que la région des Grands Fonds apparaît nettement plus favorable aux Mollusques: 39.7% des mares de ce secteur hébergent *B. glabrata* contre 19.1% seulement pour la région Est et Nord (Tableau 1). Ce phénomène s'explique vraisemblablement par les différences de régime hydrique qui ont été évoquées précédemment. La région des Grands Fonds est en effet plus arrosée que l'Est et le Nord à cause de ses reliefs sensiblement plus élevés. D'autre part, dans cette zone, les mares sont la plupart du temps situées au fond de dépressions humides et ombragées qui favorisent la permanence des eaux et des peuplements faunistiques qu'elles hébergent. Globalement, les périodes d'assèchement des mares sont donc plus importantes dans l'Est et le Nord que dans les Grands Fonds. Ces périodes, très variables selon les années, peuvent avoir des conséquences

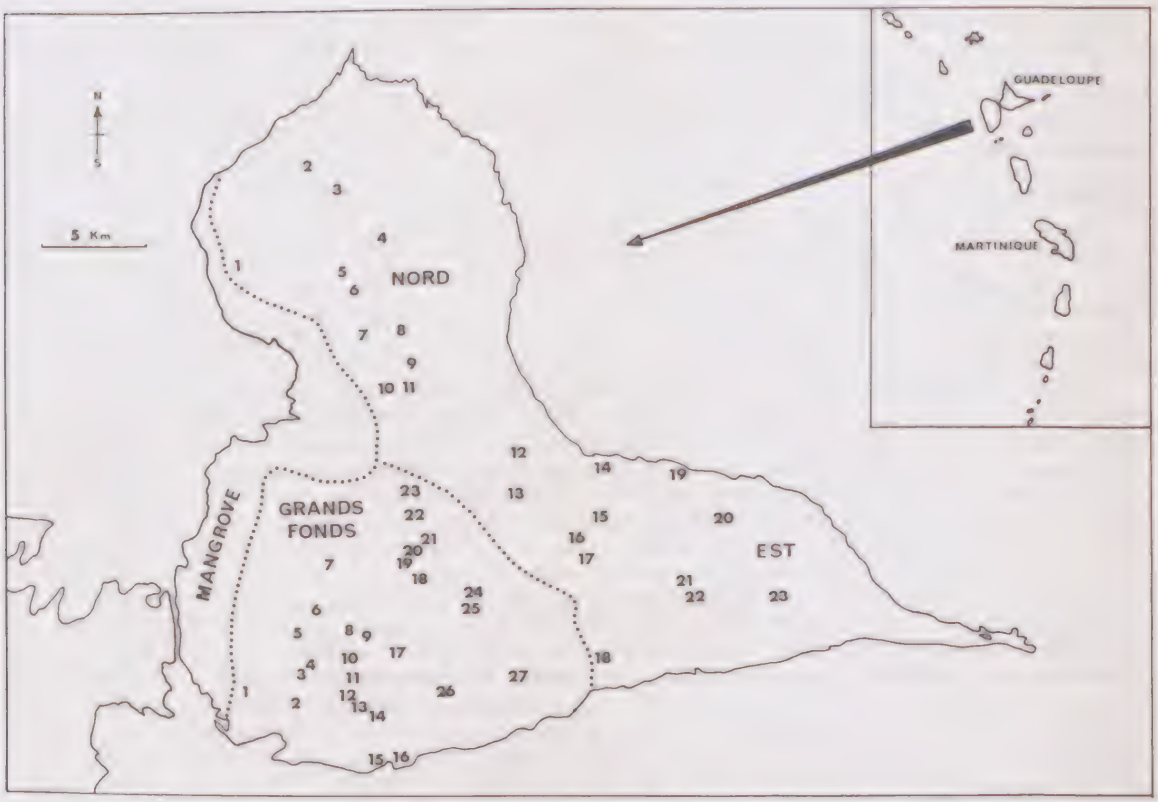

FIG. 1. Mares hébergeant *Biomphalaria glabrata* en Grande Terre. **Zone des Grands Fonds:** 1, Mare de Duthau; 2, Mare de Réjoui; 3, Mare de Caraque no. 1; 4, Mare de Caraque no. 2; 5, Mare du Pont de Caraque; 6, Mare de Laverdure; 7, Mare de David; 8, Mare de Descareaux; 9, Mare de Céligny; 10, Mare de Lambert; 11, Mare de Leroux no. 1; 12, Mare de Leroux no. 2; 13, Mare de Tombeau; 14, Mare de Kancel; 15, Mare de Redbone; 16, Mare de St Félix; 17, Mare de Moreau; 18, Mare de Malabry; 19, Mare de Dubisquet no. 1; 20, Mare de Dubisquet no. 2; 21, Mare de Dubisquet no. 3; 22, Mare de Jabrun du Nord; 23, Mare de Espérance; 24, Mare de Cambourg; 25, Mare de Grands Fonds; 26, Mare de Jacotière; 27, Mare de Fouché. **Zone Nord et Est:** 1, Mare de Fauvette; 2, Mare de Beaufond; 3, Mare de Bébian; 4, Mare de l'Hermitage; 5, Mare de Beutier; 6, Mare de Beauplan; 7, Mare des Mangles; 8, Mare de Gelas; 9, Mare de D'Enjoie; 10, Mare de Balin; 11, Mare de Bazin; 12, Mare de Néron; 13, Mare Acomat; 14, Mare de La Baie; 15, Mare de Caillebot; 16, Etang Cocoyer; 17, Mare à Mam'mé; 18, Mare de Grandmaison; 19, Mare du Lotissement du Vieux Moulin; 20, Mare de Claret; 21, Mare de Celcourt; 22, Mare de Bois Vipart; 23, Mare de Devarieux.

importantes sur les populations de *B. glabrata* et conditionnent donc, en grande partie, leur répartition (Pointier & Combes, 1976). Les effets de l'assèchement des collections d'eau sur les populations de *B. glabrata* ont déjà été étudiés dans la zone néotropicale (Olivier, 1956; Barbosa & Olivier, 1958; Andrade, 1962), et de nombreuses expériences de laboratoire ont également été effectuées sur la résistance de cette espèce à l'assèchement (Olivier & Barbosa, 1956; Richards, 1963, 1967, 1968; Sturrock, 1970).

Les rythmes saisonniers dans les mares de Grande Terre

Les études qui ont été réalisées en Grande Terre en 1980-81 ont confirmé l'importance de la pluviomètrie et en particulier l'alternance saison sèche-saison humide. Les Figs. 2 et 3 présentent les résultats globaux obtenus dans les 23 mares de la région Est et Nord et les 27 mares des Grands Fonds qui hébergeaient des populations de *Biomphalaria glabrata* en 1980-81.

TABLEAU 1. Les mares de Grande Terre. Répartition de *Biomphalaria glabrata*.

Mares	Zone des Grands Fonds	Zone Est et Nord	Totaux
Nombre total de mares recensées sur la carte au 1/20,000	198	484	682
Nombre total de mares prospectées en 1980/81	68	120	188
Pourcentage de mares prospectées en 1980/81	34.3%	24.8%	27.6%
Nombre de mares hébergeant *B. glabrata*	27	23	50
Pourcentage de mares hébergeant *B. glabrata*	39.7%	19.1%	26.5%
(intervalles de confiance 95%)	(28-52%)	(12.5-27%)	(20.5-33.5%)

En 1980, la saison sèche a été particulièrement marquée et presque toutes les moyennes pluviométriques mensuelles, de janvier à juin 1980, sont inférieures aux moyennes des 10 dernières années aussi bien dans les Grands Fonds que dans l'Est et le Nord (Figs. 2 et 3 en haut). Ceci se manifeste au niveau des mares par une baisse des eaux importante qui se traduit par des valeurs moyennes de conductivités particulièrement élevées en juillet 1980 (Figs. 2 et 3 au milieu). Par la suite, les pluies reprennent normalement d'août à décembre. Les mares se remplissent à nouveau et les conductivités moyennes baissent par suite des apports d'eau de pluie.

L'année suivante, en 1981, des moyennes pluviométriques mensuelles anormalement fortes sont observées à partir d'avril, qui se reflètent parfaitement dans les mesures de conductivités des eaux. Celles-ci, après une remontée de leurs valeurs moyennes en janvier 1981 consécutive à un début d'assèchement, baissent à nouveau en juin 1981 par suite des apports massifs d'eau de pluie.

L'évolution des populations de *Biomphalaria glabrata* paraît, quant à elle, liée à l'alternance saison sèche-saison humide. En juillet 1980, les populations malacologiques dans leur ensemble sont pleinement adultes et les tailles moyennes des Mollusques sont d'environ 15 mm pour la région Est et Nord et 20 mm pour les Grands Fonds (Figs. 2 et 3 en bas). En octobre-novembre 1980, après la remise en eau des mares, on peut constater une modification de la structure en taille des populations malacologiques qui reflète bien l'apparition des nouvelles générations. Ces générations vont ensuite évoluer pour atteindre leur maturité en juin 1981. Les tailles moyennes des Mollusques sont alors d'environ 16 mm pour la zone Est et Nord et 18 mm pour les Grands Fonds (Figs. 2 et 3 en bas). Globalement, les populations de *B. glabrata* évoluent de la même manière dans toutes les régions de la Grande Terre avec l'apparition des générations de jeunes à l'automne après la remise en eau des mares. Ceci confirme les études antérieures qui avaient déjà été réalisées en Guadeloupe (Pointier, 1979).

La région des Grands Fonds apparaît la plus homogène, à la fois du point de vue hydrologique comme le montrent les faibles écarts types calculés pour les différentes mesures de conductivités des eaux, mais également du point de vue malacologique ainsi que le montre la répartition relativement régulière des classes de taille des Mollusques (Fig. 3). Au contraire, la région Est et Nord présente une plus grande hétérogénéité hydrologique et malacologique (Fig. 2).

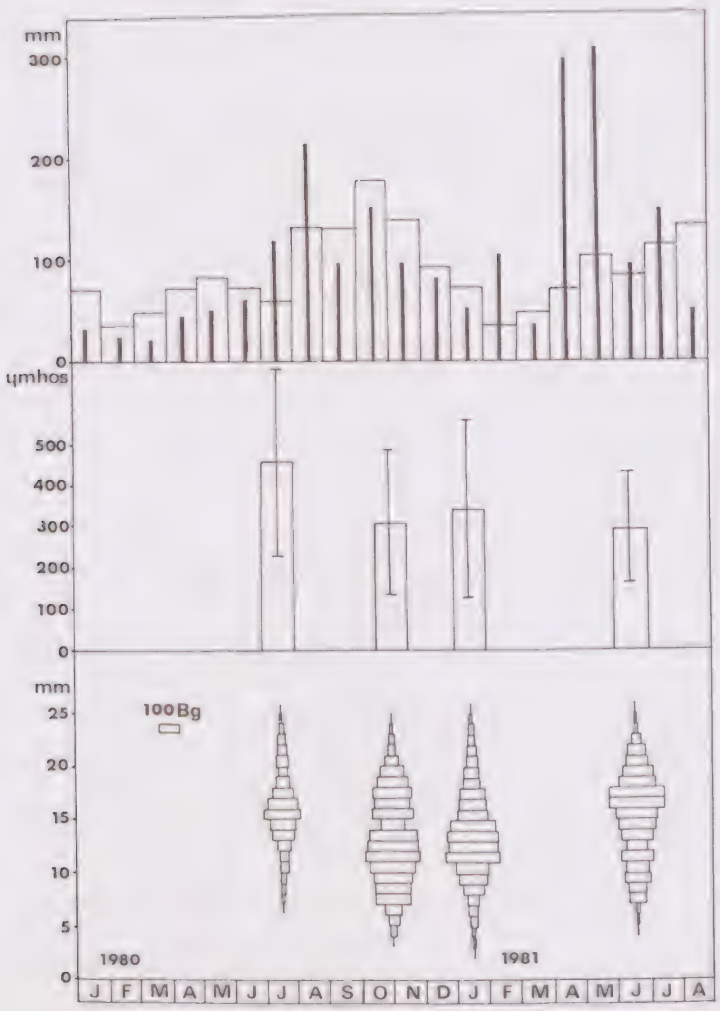

FIG. 2. Influence de la pluviométrie sur les populations de *Biomphalaria glabrata* dans 23 mares de la région Est et Nord de la Grande Terre. **En haut:** pluviométrie mensuelle moyenne, station de Saint François (histogrammes: moyennes mensuelles des 10 dernières années; bâtons: moyennes mensuelles en 1980-81). **Au milieu:** conductivités moyennes mesurées en 1980-81 dans les 23 mares de la région, les écarts types sont indiqués. **En bas:** structure en taille des populations de *B. glabrata* des 23 mares de la région.

Analyse des variables

Les analyses classiques. Les espèces liées à la présence de *Biomphalaria glabrata* sont reportées sur le Tableau 2. On peut voir que les liaisons sont nombreuses. Ces liaisons peuvent être dues à des liaisons annexes avec d'autres variables. Les variables fortement corrélées avec la présence de *B. glabrata* peuvent être considérées comme de bons indicateurs de terrain. D'autre part, les deux régions étudiées (Est et Nord et Grands Fonds) apparaissent très différentes.

Les variables végétales liées à la présence de *Biomphalaria glabrata* sont reportées sur le Tableau 3. Ce tableau montre qu'il n'existe pas d'espèce végétale dont la liaison avec *B. glabrata* nécessite un recouvrement important des mares pour être mis en évidence, c'est à dire qu'il n'y a pas de variables n'apparaissant qu'en bas du Tableau 3. Les deux variables présentes les plus régulièrement quelle que soit la région considérée, sont les Nymphéacées et la

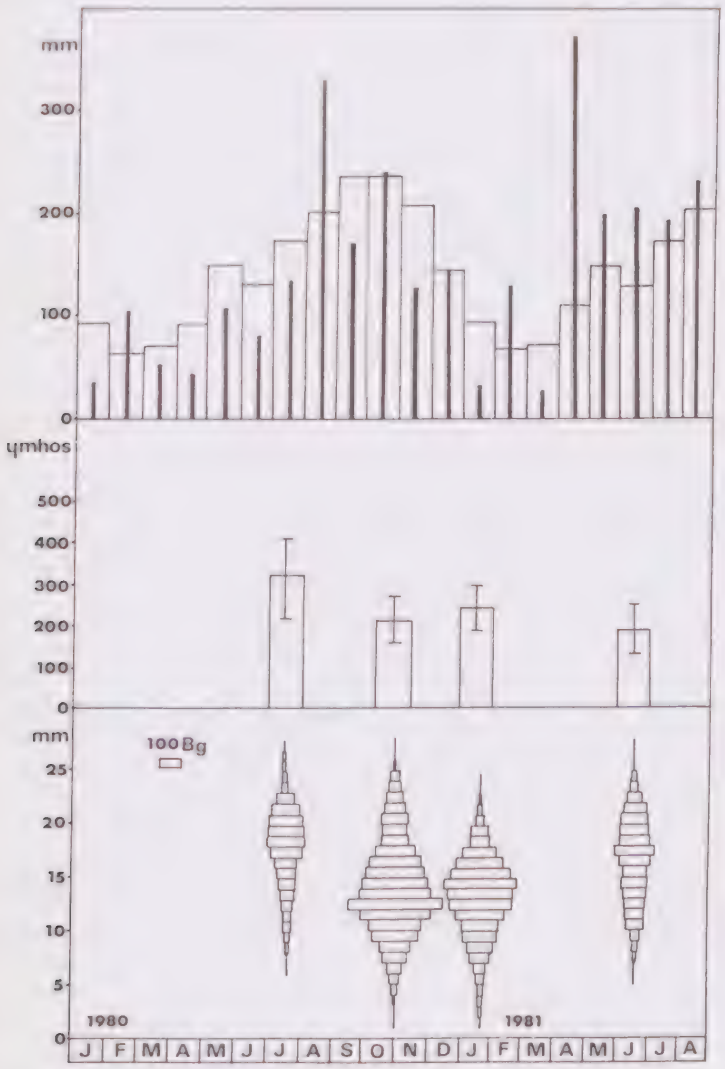

FIG. 3. **Influence de la pluviométrie sur les populations de *Biomphalaria glabrata* dans 27 mares de la région des Grands Fonds de Grande Terre. En haut:** pluviométrie mensuelle moyenne, station du Raizet (histogrammes: moyennes mensuelles moyennes des 10 dernières années; bâtons: moyennes mensuelles en 1980-81). **Au milieu:** conductivités moyennes mesurées en 1980-81 dans les 27 mares de la région, les écarts types sont indiqués. **En bas:** structure en taille des populations de *B. glabrata* des 27 mares de la région.

couverture d'arbres. Il faut cependant noter que *Ipomea palustris* n'est présente dans aucune des mares de la région des Grands Fonds.

La présence de *Biomphalaria glabrata* n'est pas liée à la date de prélèvement, le diamètre de la mare, et la conductivité de celle-ci.

L'analyse discriminante linéaire. Les espèces animales dont le coefficient de régression linéaire avec la présence de *Biomphalaria glabrata* est significativement différent de zéro figurent dans le Tableau 4. On peut voir que les autres variables de l'analyse étaient responsables de toutes les liaisons observées entre la présence de *B. glabrata* et celles des autres espèces animales (Tableau 2) à l'exception de *Drepanotrema depressissimum* (Grands Fonds),

TABLEAU 2. Espèces animales dont la présence dans les mares est liée à celle de *Biomphalaria glabrata*.

Est et Nord	Grands Fonds	Ensemble des régions
Biomphalaria schrammi **	*Drepanotrema depressissimum* ***	*P. reticulata* ***
Ampullaria glauca **		*D. depressissimum* ***
Poecilia reticulata *		*B. schrammi* **
Physa marmorata *		*D. lucidum* *
		P. marmorata *

*P < 5%; **P < 1%; ***P < 0.1%.

TABLEAU 3. Variables végétales liées à la présence de *Biomphalaria glabrata* dans les mares de Grande Terre selon le seuil de prise en compte.

Est et Nord	Grands Fonds	Ensemble des régions
	Présence/absence	
Nymphéacées ***	Nymphéacées ***	Nymphéacées ***
Ipomea palustris **	Graminées *	Couverture d'arbres ***
Cypéracées *	Polygonacées *	Couverture végétale ***
Couverture d'arbres *	Couverture d'arbres *	Graminées **
		Polygonacées *
		I. palustris *
Seuil de prise en compte de la variable végétale = 5% de recouvrement		
I. palustris **	Nymphéacées **	Nymphéacées ***
Nymphéacées **	Graminées **	Couverture d'arbres ***
Cypéracées *	Couverture d'arbres *	Graminées **
Couverture d'arbres *	Polygonacées *	Couverture végétale *
		I. palustris *
		Polygonacées *
Seuil de prise en compte de la variable végétale = 10% de recouvrement		
I. palustris *	Nymphéacées **	Nymphéacées ***
Nymphéacées *	Graminées **	Couverture d'arbres ***
Couverture d'arbres *	Cypéracées *	Graminées **
	Couverture végétale *	Couverture végétale *
		Polygonacées *
Seuil de prise en compte de la variable végétale = 20% de recouvrement		
Couverture d'arbres *	Couverture d'arbres **	Couverture d'arbres ***
	Nymphéacées *	Couverture végétale ***
	Graminées *	*I. palustris* **
	Cypéracées *	Nymphéacées **
		Graminées *
Seuil de prise en compte de la variable végétale = 50% de recouvrement		
I. palustris *		Couverture d'arbres *
		Nymphéacées *

*P < 5%; **P < 1%; ***P < 0.1%.

TABLEAU 4. Analyse discriminate linéaire. Coefficients de régression linéaires significativement différents de zéro entre la présence ou l'absence de *Biomphalaria glabrata* et celle d'autres espèces végétales ou animales dans les régions Est et Nord, les Grands Fonds ou l'ensemble des régions de la Grande Terre.

Variables	Régions		
	Est et Nord	Grands Fonds	Ensemble des régions
Nymphéacées	r = 0.27	r = 0.51	r = 0.34
Couverture d'arbres	r = 0.23	Non significatif	r = 0.23
Poecilia reticulata	Non significatif	Non significatif	r = 0.20
Drepanotrema depressissimum	Non significatif	r = 0.40	Non significatif
Cypéracées	r = -0.42	r = 0.25	Non significatif
Graminées	Non significatif	r = 0.26	Non significatif
Ipomea palustris	r = 0.37	Non significatif	Non significatif
Tilapia mossambica	r = 0.25	Non significatif	Non significatif

Poecilia reticulata (Ensemble des régions) et *Tilapia mossambica* (Est et Nord).

Nous n'avons pas d'explication particulière pour ces trois dernières liaisons qui sont probablement dues à des variables non prises en compte par l'analyse comme par exemple le facteur humain. L'homme est en effet le principal facteur responsable de l'introduction de ces espèces animales dans les mares de Grande Terre.

En ce qui concerne les espèces végétales, on observe une liaison entre la présence de *Biomphalaria glabrata* et celle des Nymphéacées (toutes les régions), des Graminées (Grands Fonds), des *Ipomea palustris* (Est et Nord), et de la couverture d'arbres (Est et Nord).

Les liaisons avec les Nymphéacées, les Graminées et les Convolvulacées sont facilement interprétables lorsque l'on sait que ces plantes offrent abri, nourriture et sites de pontes pour les Mollusques (Wright, 1956; Pointier, 1979).

La liaison avec la couverture d'arbres dans les régions Est et Nord est également facilement interprétable. Ces régions sont en effet les plus chaudes de la Grande Terre et la température des eaux des mares peut y constituer un facteur limitant aux populations de *Biomphalaria glabrata* (Pointier, 1979).

La liaison négative avec les Cypéracées dans les régions Est et Nord pose un problème et nous n'avons pas d'explication satisfaisante.

Les Trématodes parasites de *Biomphalaria glabrata* dans les mares de Grande Terre

L'étude du parasitisme de *Biomphalaria glabrata* a montré que ce Mollusque joue le rôle d'hôte intermédiaire pour huit espèces de Trématodes parasites d'Oiseaux et de Mammifères (Tableau 5). Les cycles biologiques de plusieurs de ces espèces ont été décrits récemment en Guadeloupe par Nassi (1978, 1980) et Nassi & Bayssade-Dufour (1980). Les prévalences moyennes observées pour ces huit espèces sont également présentées (Tableau 5) et s'échelonnent de 0.4% pour les plus faibles (*Apharyngostrigea* sp.) à 11.3% pour les plus élevés (*Ribeiroia marini guadeloupensis*). Les Trématodes parasites les plus répandus sont *Echinostoma* sp., *R. m. guadeloupensis* et *Clinostomum golvani*. Les plus rares sont *Strigea* sp., *Apharyngostrigea* sp. et *Petasiger caribbensis* qui n'ont été récoltés que dans une mare au cours de la saison 1980-81 (Tableau 5).

Une estimation des fluctuations saisonnières de ces parasites est présentée (Fig. 4) où nous avons fait figurer le nombre total de mares dans lesquelles ont été récoltés les divers parasites aux quatre périodes de prélèvements qui ont été effectués. On constate que le nombre de

TABLEAU 5. Trématodes parasites de *Biomphalaria glabrata* rencontrés dans les 50 mares de la Grande Terre qui hébergent le Mollusque.*

Trématodes parasites de *Biomphalaria glabrata*	Pourcentages de mares hébergeant les parasites	Prévalence moyenne observée %	Nombre de récoltes effectuées entre juillet 1980 et juin 1981
Echinostoma sp.	20%	6.2%	12
Ribeiroia marini guadeloupensis	16%	11.3%	16
Clinostomum golvani	8%	2.3%	8
Gigantobilharzia sp.	6%	1.9%	3
Apatemon (A.) graciliformis	4%	2.0%	2
Strigea sp.	2%	0.6%	3
Petasiger caribbensis	2%	9.7%	1
Apharyngostrigea sp.	2%	0.4%	1
Schistosoma mansoni	0	0	0

*On notera l'absence de *Schistosoma mansoni*.

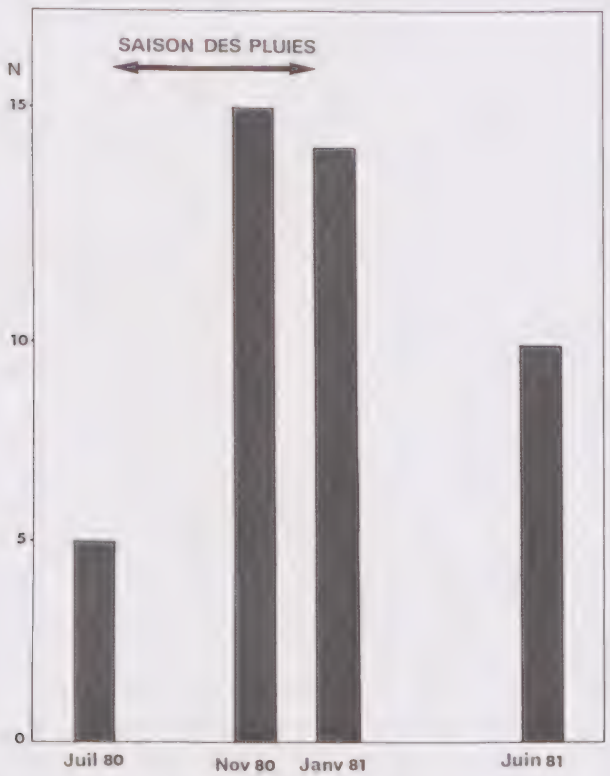

FIG. 4. Nombre de mares de Grande Terre hébergeant les huit espèces de Trématodes parasites de *Biomphalaria glabrata* à quatre périodes différentes de l'année.

mares hébergeant des parasites est nettement plus élevé en saison humide qu'en saison sèche. D'autre part, la transmission de ces parasites n'est pas interrompue au cours de la saison sèche (tout au moins en ce qui concerne les espèces les plus courantes) malgré les conditions de milieu défavorables et notamment les températures élevées qui peuvent être observées à cette période (Pointier et al., 1977; Pointier, 1979).

Les collections d'eau de la Grande Terre permettent donc la transmission des maladies parasitaires dues aux Trématodes (Tableau 6) et plus particulièrement pendant la saison des

TABLEAU 6. Répartition des Trématodes parasites de *Biomphalaria glabrata* dans les mares de Grande Terre. On notera l'absence de *Schistosoma mansoni*.

TREMATODES PARASITES DE BIOMPHALALARIA GLABRATA	MARES HEBERGEANT LES TREMATODES
SCHISTOSOMA MANSONI	
STRIGEA SP	BALIN
APHARYNGOSTRIGEA SP	BALIN
PETASIGER CARIBBENSIS	NERON
APATEMON GRACILIFORMIS	CELIGNY, DUTHAU
GIGANTOBILHARZIA SP	DUBISQUET 2, FAUVETTE, L'HERMITAGE
CLINOSTOMUM GOLVANI	MALABRY, CELIGNY, CARAQUE 3, NERON
RIBEIROIA MARINI GUADELOUPENSIS	LAMBERT, ST FELIX, CARAQUE 3, LEROUX 1, FAUVETTE, GELAS, DUTHAU, ACOMAT
ECHINOSTOMA SP	CARAQUE 2, COCOYER, REDBONE, CLARET, FAUVETTE, L'HERMITAGE, DUTHAU, BALIN, BAZIN, CAILLEBOT

pluies et le carême. Ceci contraste de manière frappante avec l'absence totale de *Schistosoma mansoni* de ces gîtes. Cette absence peut s'expliquer par trois hypothèses exclusives ou non les unes des autres: 1) présence en Grande Terre de souches de *Biomphalaria glabrata* particulières, incapables de transmettre *S. mansoni*; 2) impossibilité pour *S. mansoni* de se développer dans les conditions de milieu de la Grande Terre; 3) existence d'un processus empêchant la contamination des Mollusques. Ces trois hypothèses ont fait l'objet de recherches particulières dont les résultats seront exposés dans un prochain article.

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A NEW SPECIES OF *PUNCTUM* (GASTROPODA: PULMONATA: PUNCTIDAE) FROM THE KLAMATH MOUNTAINS, CALIFORNIA, AND FIRST CALIFORNIAN RECORDS OF *PLANOGYRA CLAPPI* (VALLONIIDAE)

Barry Roth

ABSTRACT

Punctum (Toltecia) hannai, n. sp., is described from the vicinity of Trinity Alps Camp, north of Weaverville, Trinity County, California, U.S.A., and from localities in the central Sierra Nevada. It is similar to *P. (T.) pusillum*, a species widespread in western North America, as well as Europe and Asia, and also to *P. (T.) vitreum*, from eastern North America. *Planogyra clappi* occurs in the vicinity of Trinity Alps Camp, and near Little River, Mendocino County, California – the first reported occurrences of this species south of Oregon.

INTRODUCTION

In connection with a series of studies on mollusks in the southern part of the Klamath Mountains (of which Roth & Eng (1980) and Roth & Pressley (1983) are the previous contributions), the few existing museum collections of minute snails from the region have been reviewed. The Klamath Mountains are a center of land mollusk endemism. Because they preserve vegetation and climate more like those of the later Cenozoic than does any other region in western North America (Whittaker, 1961; Axelrod, 1976), the Klamaths are of particular bearing on the Tertiary history of land mollusk faunas in the west. Collections made by the late G Dallas Hanna in the region of Trinity Alps Camp, north of Weaverville, Trinity County, California, U.S.A., yielded a previously unrecognized species of *Punctum*, described herein, and the first reported Californian occurrence of *Planogyra clappi* (Pilsbry 1898). A second occurrence of *P. clappi*, along the coast of Mendocino County, is reported. The new *Punctum* also occurs at two localities in the central Sierra Nevada.

The following institutional abbreviations are used: ANSP, Academy of Natural Sciences of Philadelphia; BMNH, British Museum (Natural History); CAS, California Academy of Sciences; FMNH, Field Museum of Natural History; LACM, Los Angeles County Museum of Natural History; RMNH, Rijksmuseum van Natuurlijke Historie, Leiden; USNM, U.S. National Museum of Natural History, Smithsonian Institution.

Genus *Punctum* Morse 1864

Type species: *Helix minutissima* Lea 1841; original designation

"Shell very minute, umbilicate, subdiscoidal with convex spire; unicolored; sculpture of oblique, delicate striae with or without spaced riblets, and excessively minute spiral striae; whorls about 4, convex, the first 1½ smooth or lightly striate spirally, rather distinctly demarked from those following, the last whorl cylindric. Aperture lunate-rounded, the lip simple and thin . . . Lung with branched pulmonary vein. Kidney U-shaped, the branch along the hind gut about equal to that along the pericardium, the ureter following the anterior border of kidney, continuing as a secondary ureter nearly to the peristome" (Pilsbry, 1948: 641). Periostracal ribs simple lamellae, major radials underlain by swelling of calcareous layer (Solem, 1977).

Subgenus *Toltecia* Pilsbry 1926

Type species: *Thysanophora (Toltecia) jaliscoensis* Pilsbry 1926; original designation

"Minute species in which most of the first whorl is smooth, rather widely spaced spirals appearing on its last fourth, continuing on the following whorl. Neanic and last whorls have a sculpture of fine and coarser growth wrinkles and indistinct riblets, and over all very fine impressed spiral lines" (Pilsbry, 1926: 116).

"Shell with major riblets widely spaced and prominent, with several, usually five or more. minor growth threads in each interval" (Pilsbry, 1948: 649).

Punctum (Toltecia) hannai, new species
Figures 1, 2A-C

Diagnosis. *Punctum (Toltecia)* with translucent, light colored, tightly coiled whorls, 2-10 (usually 5) minor radials between major radial riblets, and spiral microsculpture of parallel cords strongest around umbilicus.

Description of holotype. Shell minute, thin, translucent, light brown, depressed-turbinate; umbilicate, umbilicus contained 3.9 times in diameter. Spire convex, suture deeply impressed. Embryonic whorls 1.5, strongly demarcated from following whorls, initial 1/3 turn smooth, thereafter with very fine raised spiral lirae. Beginning of teleoconch marked by sudden increase in diameter. Sculpture of laminar major radial riblets extending obliquely from suture to interior of umbilicus, forwardly convex on shoulder, slightly sinuous on base; with 2-10 (most often 5) minor riblets in the intervals. Spiral microsculpture of parallel cords, mostly finer than radial riblets, strongest on inner portion of base and continuing into umbilicus,

FIG. 1. *Punctum (Toltecia) hannai*, new species. Apertural, top and basal views of paratype, CAS 037050; diameter 1.34 mm.

where they reticulate with minor radials. Last whorl not markedly descending behind aperture. Aperture depressed-lunate, moderately oblique; peritreme simple, inner lip slightly produced and expanded toward umbilicus. Parietal wall simply calloused, showing radial sculpture of previous whorl. Diameter 1.31 mm, height 0.81 mm, diameter of umbilicus 0.34 mm; whorls 3.6.

Type material. Holotype: CAS 037043 (shell); CALIFORNIA: Trinity County: west side of stream 0.5 to 0.75 mi [0.8 to 1.2 km] north of Trinity Alps Camp on Stuart Fork, Trinity River, elevation 3000 ft [900 m] [NW¼ NE¼ sec. 28, T. 35 N, R. 9 W, Mount Diablo Base and Meridian], G D. Hanna coll., June 1931.

Paratypes: CAS 037051 (37 shells), same locality as holotype; figured paratypes, CAS 037044, 037045 and 037050, same locality as holotype. Additional paratypes (two each) deposited in ANSP, BMNH, FMNH, LACM, RMNH and USNM.

Referred material. CALIFORNIA: Tuolumne County: 2 mi [3.2 km] north of Columbia on road to Italian Bar [SE¼ sec. 1, T. 2 N, R. 14 E, Mount Diablo Base and Meridian], G D. Hanna and E. Rixford coll., 1921 (one specimen; CAS 037049).

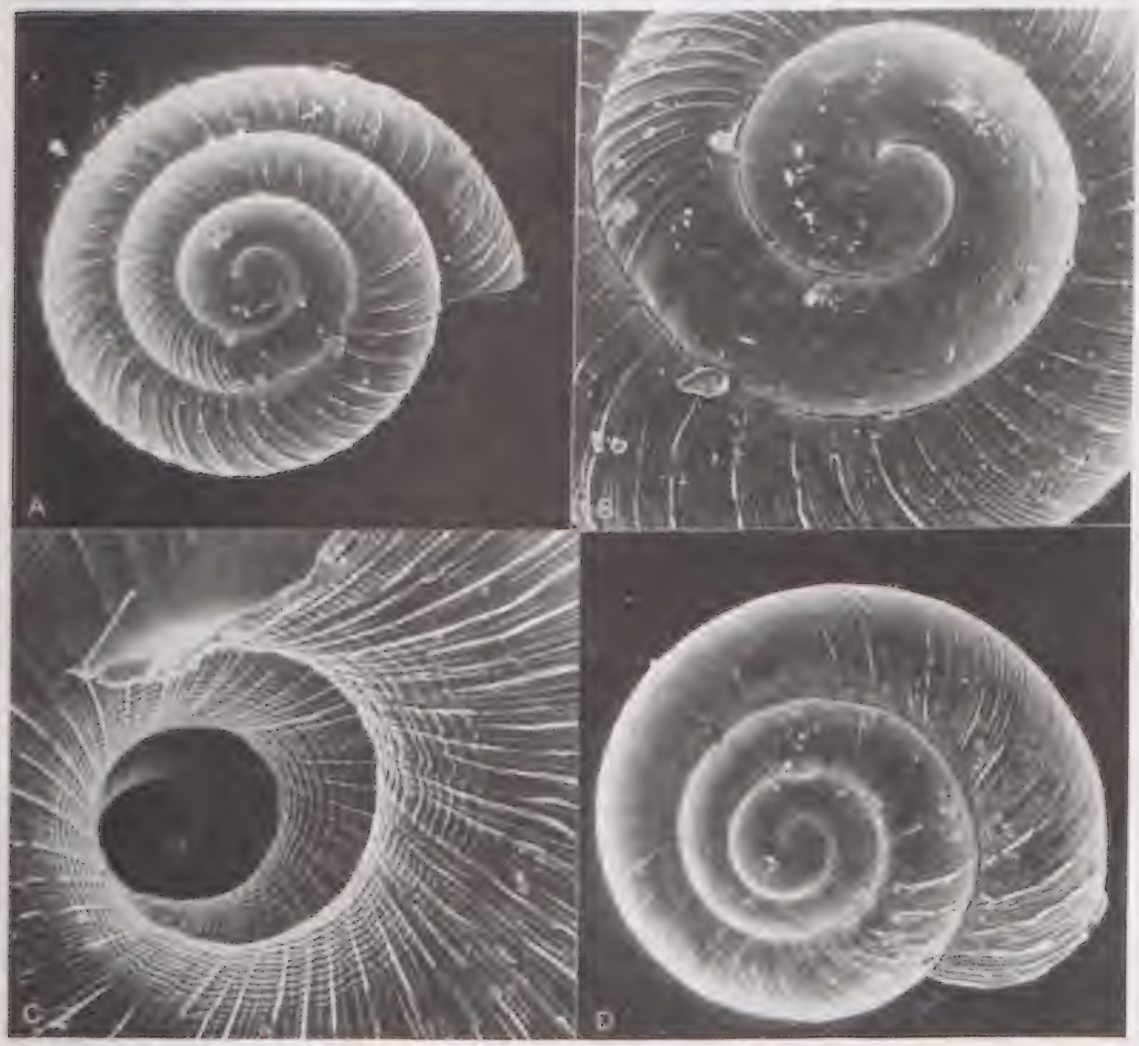

FIG. 2. A-C, *Punctum (Toltecia) hannai*, new species. A, B, Paratype, CAS 037045, top view, X43, and apical whorls, X107. C, Paratype, CAS 037044, basal sculpture, X107. D, *Planogyra clappi* (Pilsbry), California: Trinity County: 6.4 km west of Trinity Alps Camp, CAS 036853, X47.

CALIFORNIA: Mariposa County: swamp below Wawona Checking Station, Yosemite Valley, Yosemite National Park [projected sec. 33, T. 2 S, R. 21 E, Mount Diablo Base and Meridian], A.G. Smith coll., 29 June 1923 (14 specimens; CAS 037048).

Additional description. The 53 specimens in the type lot range from 0.84-1.41 mm in diameter, with 2.7 to 3.7 whorls. Most specimens of 3.5 whorls and over show a slight expansion of the peritreme inward toward the umbilicus (Fig. 2C). This probably represents a terminal phase of growth and may signify reproductive maturity. There is also minor variation in relative spire height.

The referred specimens from Yosemite Valley range from 1.09-1.53 mm in diameter, with 2.8 to 3.9 whorls. In sculpture and coiling they show no significant differences from the type lot. The referred specimen from north of Columbia is 1.34 mm in diameter, with 3.6 whorls; many of the major radials are more closely spaced than on the other material.

Many of the specimens in the type lot were alive when collected, but all soft parts are too badly deteriorated to be rehydrated for dissection.

Discussion. *Punctum (Toltecia) hannai* resembles *P. (T.) pusillum* (Lowe 1831), a widespread species best known in North America under the synonymous name *P. conspectum* (Bland 1865) (Roth, 1984). *P. pusillum* is larger (frequently more than 2 mm in diameter), darker colored, and less tightly coiled, so that the umbilical diameter is usually 28-30% of shell diameter compared to about 26% in *P. hannai*. The aperture is more rounded, less lunate, owing to the lesser encroachment of the body whorl upon the penult. In *P. pusillum* the shoulder of the whorl is often distinctly flattened, resulting in an almost angular periphery, rather than an evenly rounded profile as in *P. hannai*; the suture is generally less deeply impressed. I am not aware of any records of *P. pusillum* from the Klamath Mountains, but it occurs in the Sierra Nevada and Cascade Ranges, at both high and foothill elevations.

Punctum (Toltecia) vitreum Baker 1930, from eastern North America, is similar in color, size and whorl profile and also has up to 10 minor radials between major riblets; these form an overall reticulation where they intersect the microspiral cords. Reticulation in *P. hannai* is confined to the inner quadrant of the base. In addition, the umbilicus of *P. vitreum* is wider, about 30% of shell diameter.

The spiral liration on the protoconch and the presence of five or more minor radials per interval distinguish *Punctum hannai* from members of the typical subgenus *Punctum sensu stricto*, such as *P. (P.) randolphi* (Dall 1895) and *P. (P.) californicum* Pilsbry 1898. *P. randolphi* occurs in neighboring parts of the Klamath Mountains: Carrville, Trinity County (CAS 037046), 4 mi [6.4 km] west of Trinity Alps Camp (CAS 037047; see discussion of this locality under *Planogyra clappi*, below), and along an unnamed tributary to Packers Creek, SW¼ NE¼ sec. 36, T. 33 N, R. 12 W, Mount Diablo Base and Meridian (CAS 037052). In these lots, the umbilicus is narrower, the spire higher, radial ribbing more delicate and spiral microsculpture less pronounced than in *P. hannai*. For rapid identification, the wider umbilicus of *P. hannai* is probably the best distinguishing character.

At many other localities in and around Yosemite Valley, a *Punctum* tentatively identified as *P. californicum* is present. The distinction between this nominal taxon and *P. randolphi* is not yet clear. (Pilsbry (1948: 648) remarked that *P. californicum* is "closely similar to *P. randolphi*, and with further study may possibly turn out to intergrade fully with that.") In these lots, the narrower umbilicus, higher spire, darker brown coloration and finer radial ribbing distinguish "*P. californicum*" from *P. hannai*.

The material at hand indicates that *Punctum hannai* is an uncommon, localized species with a disjunct range divided between the Klamath Mountains and Sierra Nevada. However, the distribution of the minute land mollusks of California is very inadequately known and, once recognized, *P. hannai* may turn out to be far more common and widespread than now indicated.

The species is named for its discoverer, G Dallas Hanna, long a contributor to the knowledge of west American land mollusks.

Californian Records of *Planogyra clappi*

Referred material. CALIFORNIA: Trinity County: "0.5 mi [0.8 km] north of Kinney's Camp on line of old La Grange Ditch, 4 mi [6.4 km] west of Trinity Alps Camp"; G D. Hanna coll., June 1931 (28 specimens; CAS 036853) (Fig. 2D).

CALIFORNIA: Mendocino County: Little River, J. Helfer coll., 3 May 1935 (one specimen; CAS 037042).

These are the first records of *Planogyra clappi* (Pilsbry 1898) from the state of California. The occurrence in the Klamath Mountains of Trinity County is a range extension some 280 km south from Salem, Oregon, the southernmost previous record (Pilsbry, 1948). The town of Little River is on the Pacific coast about 120 km farther south-southwest. The Trinity County locality, here transcribed from the CAS locality register, contains an apparent inconsistency, as the facility known at present as Kinney Public Camp is approximately 2 km due south of the resort community of Trinity Alps [USGS Trinity Dam, Calif., Quadrangle, 15-minute Series (Topographic), ed. 1950]; the abandoned La Grange Ditch is about 3-3.5 km west of either, at an elevation of 3700 ft [1100 m].

Sixteen of the 28 shells in the Trinity County lot virtually lack upstanding periostracal laminae; others have them well developed. This is evidently a wear phenomenon, to judge by the selective presence of laminae on adjacent parts of two whorls (Fig. 2D).

The previously known range of *Planogyra clappi* is from British Columbia (Nanaimo; Quamicham District, Vancouver Island), Canada, to Salem, Oregon, U.S.A. (Pilsbry, 1948; CAS). The southernmost Oregonian locality in the CAS collection is House-on-the-Metolius, near Camp Sherman, Jefferson County, A.G. Smith coll., July 1968 (CAS 036852) (one *P. clappi* in large lot of *Punctum pusillum* obtained by trapping). Pilsbry remarked on the wide disjunction between *P. clappi* and the eastern species *Planogyra asteriscus* (Morse 1857), which is found in New England and in states and provinces bordering on the St. Lawrence and Great Lakes drainage.

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AN ADVANTAGEOUS USE OF MULTIVARIATE STATISTICS IN A BIOMETRICAL STUDY ON THE *ARION HORTENSIS* COMPLEX (PULMONATA: ARIONIDAE) IN BELGIUM

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ABSTRACT

Three hundred and forty-six specimens of *Arion hortensis* s.l. were dissected and scored for 15 characters using multivariate statistics in order to investigate morphological variation in this slug complex in Belgium. The data obtained were analyzed with a canonical variate analysis and a principal component analysis. Both showed that the material comprised two forms, corresponding to *A. hortensis* s.s. and *A. distinctus*. The most reliable features to distinguish these forms in Belgium appear to be the structure associated with the outlet of the epiphallus in the atrium and the presence or absence of an eversible portion in the oviduct. However, even after exclusion of these characters from the analyses, a fairly good segregation of both forms was seen.

INTRODUCTION

In recent years, slugs formerly known as *Arion hortensis* Férussac 1819 have been divided into three distinct species, viz., *A. hortensis* s.s., *A. distinctus* Mabille 1868 and *A. owenii* Davies 1979, which differ in their genitalia, spermatophores, mating behaviour and, to a lesser extent, in their external morphology (Davies, 1977, 1979; Backeljau, 1981; De Wilde, 1983). Despite these differences, however, it is often very difficult to distinguish the three species because they show a lot of morphological overlap. Hence, *A. hortensis* s.l. may be considered as a complex of sibling species.

The present paper investigates the morphological variation in *Arion hortensis* s.l. and demonstrates that in such studies a biometrical and multivariate approach can be most instructive. As far as we know, this is the first time that this kind of analysis has been performed on slugs. Since only *A. hortensis* s.s. and *A. distinctus* occur in Belgium (Backeljau, 1981; De Wilde, 1983), and since these two species particularly are very similar, we will confine ourselves here to their study.

MATERIAL AND METHODS

Three hundred and forty-six preserved specimens (70% ethanol) of *Arion hortensis* s.l. from 128 U.T.M. (Universal Transverse Mercator) squares in Belgium were examined (Table 1). The material was collected throughout each year (1977-1980) in various kinds of habitats (Marquet, 1982). Only those specimens which after dissection proved to contain fully developed genitalia were considered. Each individual was then scored for the following characters. **External:** (1) the color of the back in comparison with arbitrarily chosen reference specimens (dark/light); (2) the orientation of the lateral bands on the head side of the mantle (Fig. 1); (3) the path of the right lateral band around the pneumostome (Fig. 2); (4) the position of the lateral bands on the sides of the body (above, below or on the middle of the flank); (5) the visibility of the lateral bands on the contracted slugs seen from above (distinct/marginal); (6) length of the mantle (Fig. 1); (7) breadth of the mantle (Fig. 1); (8) distance between the lateral bands on the head side of the mantle (Fig. 1); (9) distance between the lateral bands on the mantle near the pneumostome (Fig. 1); **Internal:** (10) pigmentation of the epiphallus (present/absent); (11) length of the eversible portion in the oviduct (Fig. 3); (12) length of the firm portion in the oviduct (Fig. 3); (13) length of the distal channel in the oviduct (Fig. 3); (14) thickening around the outlet of the pedunculus in the atrium (present/absent) (Fig. 3); (15) type of the structure associated with the outlet of the epiphallus in the atrium, here further referred to as ES (= epiphallus structure) (Fig. 4). The choice of these characters was based chiefly on the papers of Davies (1977, 1979).

TABLE 1. Data matrix of the 346 specimens studied. The character numbers above each column are the same as those used in the text.* (Measurements are given in 0.1 mm.)

catalog number	15*	1	2	3	4	5	6	7	8	9	10	11	12	13	14
3395.01	dist	4	2	6	6	9	69	27	10	14	5	10	20	27	10
3395.02	dist	8	2	6	2	1	64	62	10	15	4	10	28	38	10
3395.03	dist	8	3	7	2	1	61	63	10	14	4	10	21	47	11
3395.04	dist	8	2	7	2	1	59	61	14	19	4	10	21	35	10
3315.03	dist	8	2	8	3	1	70	51	10	22	4	10	38	39	9
2851.01	dist	4	3	6	4	9	64	49	10	21	4	10	21	21	9
1219.05	dist	4	3	4	4	2	61	41	10	19	4	10	20	41	10
1219.02	dist	4	3	4	3	1	59	41	13	17	4	10	20	30	9
1219.03	dist	8	3	4	4	1	59	41	14	18	4	10	19	18	9
1219.01	dist	4	2	3	4	2	63	41	13	18	4	10	15	31	9
1376.03	dist	4	2	5	4	9	68	59	11	14	4	10	20	30	9
1376.02	dist	4	2	4	3	9	66	56	11	18	4	10	17	28	9
0216.01	dist	8	2	2	4	2	61	59	14	21	4	10	36	29	9
0093.01	dist	4	3	3	4	2	61	58	10	19	4	10	24	31	9
0439.01	dist	4	3	4	4	9	64	58	13	19	4	10	26	36	9
0180.01	dist	4	2	4	3	9	69	60	10	24	4	10	20	39	9
0180.02	dist	4	2	4	4	9	66	58	10	29	4	10	12	37	9
0180.03	dist	4	2	3	3	2	59	58	10	25	4	10	19	40	9
0180.04	dist	4	2	3	4	2	60	59	10	31	4	10	22	27	9
0260.01	dist	4	3	4	3	9	70	59	10	34	4	10	20	38	9
1046.02	dist	4	2	4	4	2	59	59	10	31	4	10	21	41	9
0422.02	dist	4	2	4	4	1	61	58	10	25	4	10	20	39	9
0422.03	dist	4	2	4	4	1	64	58	10	25	4	10	26	17	9
0422.04	dist	4	2	4	4	2	66	58	10	29	4	10	20	33	9
1252.01	dist	4	3	4	3	9	64	59	12	19	4	10	15	44	9
1252.02	dist	4	2	4	4	2	60	61	11	16	4	10	12	23	9
1252.03	dist	4	2	4	4	1	66	60	10	13	4	10	24	29	9
1252.04	dist	4	2	4	3	9	63	60	11	14	4	10	15	17	9
2325.02	dist	4	2	4	4	2	67	66	12	27	4	10	22	35	9
2282.03	dist	4	3	4	4	1	66	61	10	22	4	10	20	08	9
0048.01	dist	4	3	4	4	1	64	59	11	25	4	10	25	40	9
0206.02	dist	4	2	4	4	9	63	60	11	20	4	10	27	30	9
0206.01	dist	4	2	4	4	1	63	56	11	18	4	10	26	42	9
0106.01	dist	4	3	4	4	9	69	67	11	30	4	10	24	39	9
0064.01	dist	4	3	4	4	2	71	64	10	29	4	10	31	33	9
0076.01	dist	4	3	4	4	1	74	69	10	26	4	10	36	34	9
0164.01	dist	4	2	4	4	1	67	61	11	19	4	10	25	29	9
0263.01	dist	4	2	4	4	1	66	58	11	24	4	10	22	19	9
1376.01	dist	4	2	4	4	9	68	56	11	18	4	10	25	42	9
0753.01	dist	4	2	4	4	1	70	60	11	21	4	10	32	35	9
2740.03	dist	4	2	4	4	1	66	56	10	19	4	10	28	33	9
0110.01	dist	4	3	4	3	9	61	59	10	26	4	10	22	47	9
0071.11	dist	4	3	4	4	1	64	61	10	26	4	10	35	49	9
1820.01	dist	4	3	4	4	1	68	56	10	19	4	10	27	40	9
1820.02	dist	4	3	4	4	1	67	59	11	23	4	10	31	33	9
0199.02	dist	4	2	4	4	1	68	60	11	20	4	10	20	31	9
2401.05	dist	4	3	4	4	9	71	64	11	21	4	10	24	18	9
1821.02	dist	4	3	4	4	1	70	56	11	21	4	10	21	40	9
2401.08	dist	4	3	4	4	9	66	56	11	24	4	10	32	36	9
2852.03	dist	4	3	4	4	9	66	59	11	17	4	10	30	34	9
2852.02	dist	4	3	4	3	1	64	56	10	13	4	10	33	30	9
2852.01	dist	4	2	4	4	1	67	59	10	16	4	10	24	26	9
2747.03	dist	4	3	4	4	9	63	61	11	15	4	10	20	31	9
2747.02	dist	4	2	4	4	1	60	59	10	15	4	10	20	31	9
2697.02	dist	4	3	4	4	9	63	61	11	15	4	10	35	33	9
2697.01	dist	4	3	5	4	1	61	59	11	19	4	10	28	25	9
2731.04	dist	4	2	4	4	1	60	59	10	13	4	10	28	16	9
2731.03	dist	4	2	4	4	1	60	56	10	22	4	10	22	30	9
2731.01	dist	4	2	4	4	1	63	59	10	21	4	10	37	37	9
0950.02	dist	4	2	4	3	9	63	61	11	20	4	10	14	34	9
1987.01	dist	4	2	4	4	1	63	60	10	23	4	10	27	33	9
1987.02	dist	4	2	4	4	1	64	61	10	24	4	10	25	29	9
1987.04	dist	4	2	4	4	9	59	57	10	15	4	10	24	41	9
2069.02	dist	4	3	4	4	1	63	59	10	16	4	10	15	28	9
2069.01	dist	4	3	5	4	1	63	59	10	16	4	10	15	28	9
2115.01	dist	4	3	5	4	1	63	61	10	18	4	10	20	38	9
1788.02	dist	4	3	4	4	1	63	59	10	20	4	10	25	39	9
1872.01	dist	4	3	5	4	9	66	59	10	18	4	10	30	43	9
1889.04	dist	8	2	4	4	9	63	57	10	17	4	10	25	24	9
1889.03	dist	8	3	4	4	9	63	61	11	23	4	10	23	33	9
1889.02	dist	4	3	4	4	9	70	63	11	21	4	10	27	29	9
1889.01	dist	4	3	4	4	9	70	66	10	27	4	10	19	36	9
1889.06	dist	4	2	5	4	9	66	64	11	37	4	10	37	33	9
1889.05	dist	4	3	4	4	1	60	56	10	16	4	10	20	31	9
1677.01	dist	4	3	5	4	1	60	61	10	26	4	10	18	33	9
1800.01	dist	4	3	4	4	1	68	63	11	32	4	10	31	34	9
1800.02	dist	4	2	4	4	9	68	59	10	30	4	10	20	39	9
2239.11	hort	4	3	4	2	1	60	59	10	16	4	10	21	31	9
1880.01	dist	4	3	4	4	9	56	60	10	24	4	10	30	41	9
1869.01	dist	4	3	4	4	1	70	60	10	21	4	10	30	43	9
2262.02	hort	4	3	4	4	1	61	59	10	19	4	10	14	31	9
2239.10	hort	4	3	4	4	1	61	63	11	20	4	10	16	28	9
2239.08	hort	4	3	4	4	9	63	63	10	16	4	10	14	30	9
2239.07	hort	4	3	4	4	1	63	64	10	16	4	10	16	36	9
2245.04	dist	4	3	4	4	1	61	63	10	25	4	10	25	36	9
2268.02	dist	4	3	4	3	1	60	59	10	16	4	10	18	32	9
2268.01	hort	4	3	4	4	1	63	56	10	21	4	10	14	30	9
2259.01	dist	4	3	4	4	1	60	61	10	23	4	10	16	30	9
2078.01	dist	4	2	4	4	1	63	56	10	20	4	10	18	28	9
1618.01	dist	4	3	4	4	9	68	59	10	14	4	10	19	43	9
1812.01	dist	4	3	4	4	1	66	59	10	22	4	10	31	32	9
1660.02	dist	4	3	4	4	1	66	61	10	16	4	10	21	42	9
2747.01	dist	4	3	4	4	1	59	56	10	18	4	10	33	30	9
0194.02	dist	4	3	4	4	9	66	59	10	30	4	10	21	38	9
1812.02	dist	4	3	4	3	1	66	56	10	16	4	10	45	35	9

See end of table (p. 61) for abbreviations.

*The determinations are based on character 15 (type of ES). Note that the initial misidentifications mentioned in the text have been corrected.

catalog number	Scores														
	15	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1771.02	dist	B	C	F	K	L	41	33	14	16	0	00	15	24	Q
0216.02	dist	A	C	H	I	L	64	35	10	16	0	00	35	30	Q
0422.01	dist	A	C	F	I	L	55	35	14	21	0	00	15	27	P
0425.01	dist	A	D	F	I	L	62	35	22	24	0	00	20	25	P
1771.01	dist	B	E	F	J	L	51	33	11	13	0	00	24	30	Q
2325.07	dist	A	E	F	J	M	54	39	13	26	0	00	18	27	P
0194.01	dist	A	E	F	J	L	73	48	18	28	0	00	17	45	P
2240.02	dist	A	E	F	I	L	61	51	26	34	0	05	31	35	P
1063.01	dist	B	C	F	I	L	59	34	14	20	0	00	21	15	P
2332.01	dist	A	C	F	K	M	62	36	16	20	0	00	21	37	P
2697.03	dist	B	E	F	J	M	58	32	12	15	0	00	40	33	P
2747.04	dist	B	D	F	J	L	53	35	10	13	0	00	25	27	P
2740.01	dist	A	E	F	I	L	57	40	14	20	0	00	29	39	Q
2740.02	dist	A	C	G	K	L	50	34	15	19	0	00	23	25	P
1805.03	dist	A	C	F	J	M	58	37	15	25	0	05	33	28	P
1046.01	dist	A	E	F	K	L	74	38	16	25	0	06	18	33	P
1344.01	dist	B	C	F	K	L	61	41	18	18	0	00	32	26	Q
0982.01	dist	A	C	F	J	L	58	35	13	20	0	00	14	19	P
0982.02	dist	A	C	F	J	M	50	31	11	16	0	00	20	22	P
0932.02	dist	A	C	F	I	L	52	39	11	18	0	00	24	31	P
0932.01	dist	A	C	F	K	M	60	35	16	22	0	00	15	26	P
0934.01	dist	A	C	F	K	L	62	36	19	21	0	00	20	19	P
0929.01	dist	A	C	F	K	L	81	49	18	29	0	00	27	33	P
3357.01	dist	A	C	G	K	L	49	34	07	12	0	00	25	30	P
3357.03	dist	B	C	F	K	M	52	33	09	20	0	00	26	29	Q
3374.01	dist	A	C	F	J	M	52	39	13	18	0	00	27	28	P
3374.02	dist	A	C	F	K	L	46	35	12	14	0	00	25	29	P
3374.03	dist	A	C	F	K	M	46	35	09	15	0	00	21	40	Q
3356.01	dist	A	C	F	K	L	46	32	07	10	0	00	29	25	P
3353.01	dist	A	E	F	K	M	46	34	11	13	0	00	24	35	P
3388.01	dist	B	C	F	K	L	59	44	11	17	0	00	32	31	P
3386.01	dist	B	C	F	K	M	50	36	09	14	0	00	28	31	Q
3322.01	dist	A	D	G	I	L	61	41	20	22	0	00	24	38	P
2454.01	dist	A	C	F	I	L	69	45	17	22	0	00	20	37	P
3282.01	dist	A	E	F	J	L	75	45	18	29	0	00	30	19	P
3281.01	dist	A	D	F	J	L	48	35	20	21	0	00	24	34	P
3357.02	dist	A	C	F	K	M	41	31	11	12	0	00	24	31	P
2679.03	dist	B	C	F	J	L	57	33	15	19	0	00	20	24	P
2679.02	dist	A	C	F	I	L	55	35	13	21	0	00	25	47	P
2679.01	dist	A	C	F	I	L	42	34	14	19	0	00	17	32	P
2838.03	dist	A	C	G	I	L	60	38	12	18	0	00	17	08	P
2838.02	dist	B	D	F	K	M	44	30	12	16	0	00	15	14	Q
2838.01	dist	B	D	F	I	L	66	44	16	19	0	00	19	33	P
2665.01	dist	B	C	F	I	L	46	31	10	18	0	00	26	23	P
1828.01	dist	B	C	F	K	L	47	41	15	20	0	00	20	25	P
1855.01	dist	A	C	F	K	L	61	38	14	25	0	00	25	29	P
2590.01	dist	A	C	F	I	M	57	33	15	16	0	00	15	25	P
1839.01	dist	A	E	F	K	M	80	45	11	23	0	00	24	35	P
0641.01	dist	A	C	F	I	L	50	36	15	14	0	00	15	20	P
0891.01	dist	B	C	F	I	L	55	41	13	19	0	00	23	27	P
1013.01	dist	B	C	H	J	M	62	38	18	22	0	00	22	27	P
0939.01	dist	A	C	F	J	L	64	40	13	23	0	00	25	46	P
0832.01	dist	A	C	F	J	M	63	39	14	26	0	00	18	32	P
1027.01	dist	A	E	F	K	L	54	36	06	15	N	00	15	19	P
3165.01	dist	A	C	F	K	L	80	48	26	37	0	00	25	35	P
3159.01	dist	A	C	F	K	M	59	40	17	21	0	00	31	44	P
3187.01	dist	A	E	G	K	L	54	31	12	17	0	00	20	19	P
3154.01	dist	A	C	F	K	L	54	35	06	19	0	00	24	20	P
1388.01	dist	A	C	F	K	L	60	37	15	16	0	00	17	19	P
0913.01	dist	A	C	F	K	L	45	34	10	14	0	00	21	40	P
0825.01	dist	A	D	G	I	L	63	39	21	21	0	00	30	34	Q
0612.01	dist	A	C	F	K	M	45	35	09	12	0	00	11	21	P
0927.01	dist	A	C	F	K	M	50	32	12	19	0	00	18	38	P
1661.02	dist	A	E	F	I	L	61	43	12	24	0	00	21	25	P
1659.01	dist	A	E	F	K	L	54	34	12	17	0	00	27	35	P
1893.01	dist	A	C	F	I	L	61	35	13	17	0	00	21	43	Q
1952.01	dist	A	E	F	I	L	55	39	08	15	0	00	25	36	Q
2575.01	dist	A	C	F	I	L	49	30	11	14	0	00	24	30	P
1376.04	dist	A	E	F	K	M	41	34	09	12	0	00	15	40	Q
0939.02	dist	A	C	F	K	M	60	38	15	20	0	00	23	29	P
0939.03	dist	A	E	F	I	L	62	40	11	20	0	00	29	25	Q
1912.01	dist	A	C	F	K	M	49	35	18	23	0	00	19	27	Q
1361.01	dist	A	C	F	K	L	55	35	14	14	0	00	21	28	P
0572.01	dist	A	C	F	I	L	49	36	15	16	0	00	13	26	P
1378.01	dist	A	C	H	K	M	54	30	15	19	0	00	23	17	P
1274.01	dist	A	C	F	I	L	62	40	15	15	0	00	23	39	Q
0959.01	dist	A	C	H	K	M	60	30	15	19	0	00	15	25	P
0617.01	dist	B	C	F	K	L	75	49	26	29	0	00	19	37	P
0617.02	dist	B	C	F	K	L	50	28	14	19	0	00	14	19	Q
1008.02	dist	A	C	H	K	M	61	30	15	18	0	00	20	30	P
1008.01	dist	A	C	F	I	L	65	42	14	20	0	05	17	24	P
0670.01	dist	A	C	F	J	M	61	40	14	22	0	00	17	20	P
0681.01	dist	A	C	F	J	M	46	30	15	17	0	00	20	14	P
1383.01	dist	A	C	F	J	M	65	38	13	17	0	00	10	20	P
2801.01	dist	A	C	F	K	L	59	37	14	18	0	00	17	35	Q
2344.01	hort	A	C	F	K	L	64	40	14	17	0	24	18	28	P
2310.01	dist	A	C	F	K	M	70	31	14	19	0	00	24	22	P
1877.01	dist	A	C	F	I	L	60	41	11	24	0	00	26	44	Q
2309.01	dist	B	C	F	K	L	61	39	14	09	0	00	18	55	P
2314.01	dist	B	C	F	I	M	54	40	29	20	0	00	16	24	P
2512.01	dist	A	C	F	K	L	54	36	12	14	0	00	18	27	P
2872.01	dist	A	C	F	K	M	50	35	12	18	0	00	23	27	P
2549.01	dist	A	C	F	K	L	46	30	14	13	0	07	11	38	P
2545.01	dist	A	C	F	J	M	54	36	12	24	0	00	24	27	Q
2868.01	dist	A	C	F	K	L	70	49	24	29	0	00	27	38	P

catalog number	15	1	2	3	4	5	6	7	8	9	10	11	12	13	14
							Scores								
0590.01	dist	A	C	F	E	L	63	41	14	21	0	00	20	25	F
0043.01	dist	A	E	F	J	L	80	42	03	25	D	00	18	27	F
1692.01	dist	A	C	F	E	L	57	33	13	19	0	00	20	36	F
1293.01	dist	B	E	G	E	M	53	31	08	17	D	01	23	26	F
1347.01	dist	A	C	F	E	L	55	36	14	19	0	00	09	22	F
2390.01	dist	A	C	F	E	L	55	39	12	16	0	00	24	48	F
2482.01	dist	A	C	F	E	M	60	35	21	15	0	00	20	24	F
0605.01	dist	A	C	F	E	M	59	29	15	20	0	00	14	16	F
1272.01	dist	A	C	F	E	M	52	36	17	20	0	00	24	27	U
2460.01	dist	A	E	F	E	M	61	35	13	21	0	00	25	34	F
3355.01	dist	A	C	F	E	M	44	31	11	11	0	06	15	23	F
2421.01	dist	A	C	F	E	L	61	41	11	15	0	00	19	15	F
2891.01	dist	A	E	F	E	M	57	35	10	18	0	00	14	25	U
2428.01	dist	A	E	F	J	L	67	37	15	15	0	00	25	18	F
2962.01	dist	A	E	F	J	L	56	33	14	15	0	02	11	18	F
2460.02	dist	A	E	F	E	L	69	40	11	15	0	00	31	15	F
2422.01	dist	A	C	F	J	M	67	41	15	15	0	00	20	63	F
0749.01	dist	A	C	F	E	L	66	40	15	16	0	00	26	36	E
0643.01	dist	A	C	C	E	L	61	33	13	17	0	00	15	20	F
0986.01	dist	A	C	F	E	L	69	36	16	21	0	00	20	12	E
2560.01	dist	A	E	F	J	E	69	36	16	15	0	00	29	60	F
1052.02	dist	A	C	F	E	L	60	34	13	19	0	00	20	33	F
2584.01	dist	A	C	F	J	M	62	40	17	19	0	00	25	27	E
2693.01	dist	A	E	F	J	M	66	40	14	24	0	00	15	19	F
2669.01	dist	A	C	F	E	L	64	39	11	19	0	00	27	30	F
2350.01	dist	A	C	F	J	M	58	37	13	20	N	00	20	38	F
2467.01	dist	B	C	F	E	L	56	35	12	14	0	00	21	23	F
2239.15	dist	A	C	F	J	M	53	26	11	19	0	00	20	23	F
2675.01	dist	A	E	C	E	L	66	42	16	24	0	00	28	39	F
2756.01	dist	A	C	F	E	M	60	40	15	19	0	00	22	40	Q
1222.01	dist	A	E	F	J	L	60	41	13	18	0	00	19	42	Q
1043.01	dist	A	C	F	E	L	55	40	16	26	0	00	17	41	F
1549.01	dist	B	C	F	J	L	49	27	12	15	0	00	16	20	Q
1141.01	dist	A	C	F	E	L	66	42	17	24	0	00	23	39	Q
3358.01	dist	A	C	F	E	M	42	31	09	11	0	00	21	28	F
1098.01	dist	A	C	F	J	L	61	36	16	18	0	00	34	37	C
1142.01	dist	A	C	F	E	M	54	35	19	18	0	00	18	30	F
1139.01	dist	A	C	F	J	M	49	36	15	18	0	00	22	17	F
1585.01	dist	A	C	F	E	L	47	30	09	12	0	00	17	10	F
3315.02	hort	B	E	F	E	L	58	37	12	25	0	31	24	28	E
3315.01	hort	B	E	F	E	L	44	44	16	13	0	39	21	31	C
3315.04	hort	B	C	C	J	L	50	30	15	17	0	13	10	14	C
1660.05	hort	B	E	C	I	L	54	46	15	14	0	27	15	34	F
1660.03	hort	B	C	C	I	L	53	33	16	13	0	35	10	31	C
1660.06	hort	A	E	C	I	L	38	31	11	12	0	28	11	21	C
0071.03	hort	B	C	F	J	L	60	48	21	26	0	26	10	26	C
0199.03	hort	B	C	C	E	L	48	41	14	18	N	20	04	12	C
2325.05	hort	B	C	E	J	M	64	39	16	21	0	36	10	31	C
2325.03	hort	B	C	C	I	M	77	46	20	24	0	44	19	18	C
2281.05	hort	B	E	C	E	L	48	39	12	15	0	16	10	17	C
2281.07	hort	B	C	F	E	M	56	43	15	22	N	16	11	13	C
2281.03	hort	B	E	C	E	L	43	40	12	13	0	11	06	11	C
2239.01	hort	B	C	C	E	M	66	50	27	13	0	25	07	24	C
2239.02	hort	B	C	C	J	L	75	50	14	11	0	17	08	31	C
2239.05	hort	B	C	C	E	M	60	42	14	16	0	15	10	26	C
2400.02	hort	B	C	C	I	L	61	34	24	24	0	31	15	31	C
1803.01	hort	B	C	C	E	L	45	37	16	16	0	33	16	24	F
2400.05	hort	B	C	F	J	M	58	44	18	30	N	35	13	27	F
1805.02	hort	B	C	C	I	L	69	41	09	15	N	35	22	02	C
1660.04	hort	B	E	C	E	L	51	40	17	15	0	20	11	20	F
2282.01	hort	B	C	C	E	L	51	43	09	10	0	26	08	09	C
2282.02	hort	B	E	C	E	L	62	52	14	14	0	22	08	09	C
2239.04	hort	B	C	F	E	L	68	38	18	15	0	17	12	15	E
2239.03	hort	B	C	C	I	M	70	48	24	21	0	33	09	41	C
2237.02	hort	B	C	C	E	L	60	45	19	18	0	21	06	15	C
2268.03	hort	B	C	C	E	L	60	49	19	19	N	25	14	10	C
2239.06	hort	B	C	E	E	L	59	48	14	19	N	20	12	26	E
2237.01	hort	B	C	C	E	L	60	46	21	15	0	26	11	12	E
2281.06	hort	B	C	C	E	L	42	35	13	15	0	12	10	10	C
2281.09	hort	B	C	C	E	L	35	33	13	09	0	17	13	14	C
1660.01	hort	A	C	C	E	L	45	42	21	21	0	32	10	21	C
0071.13	hort	B	E	C	E	L	46	37	25	23	0	26	09	25	C
0071.12	hort	B	E	C	I	M	60	46	23	23	0	26	15	35	C
0071.10	hort	B	C	C	I	M	54	38	18	19	0	29	14	39	F
0071.09	hort	B	C	C	E	M	60	45	18	27	0	24	14	18	F
0071.08	hort	B	E	C	E	M	58	41	17	24	0	15	09	08	C
0071.07	hort	B	C	C	I	M	59	42	18	19	0	24	08	19	C
0071.06	hort	B	C	C	E	M	55	45	23	22	0	25	09	35	C
0071.04	hort	B	C	C	E	M	65	49	20	25	0	22	15	35	C
0199.01	hort	B	C	C	I	L	50	47	21	20	N	34	14	15	C
2400.04	hort	B	C	C	I	M	70	46	18	21	N	40	15	25	C
2400.03	hort	B	C	C	E	L	56	42	19	16	0	31	19	26	F
2401.04	hort	B	C	E	I	L	56	40	16	20	0	22	10	25	E
2401.03	hort	B	C	C	E	M	64	49	22	26	0	31	19	22	C
2401.02	hort	A	C	E	I	M	63	45	26	26	0	35	13	36	C
2401.01	hort	B	C	C	I	M	53	43	19	26	0	30	15	21	C
2731.05	hort	B	C	E	E	L	47	33	10	12	0	16	19	37	C
0950.01	hort	B	E	C	I	M	60	41	16	19	N	33	12	26	E
2235.01	hort	B	C	C	I	L	50	42	15	16	0	26	21	21	C
2264.01	hort	A	E	C	I	L	73	46	24	14	0	42	16	32	C
0201.02	hort	B	E	E	I	L	50	36	20	17	0	17	12	18	C
2262.01	hort	B	E	C	I	L	65	52	21	19	0	29	26	01	C
2401.07	hort	B	E	C	I	L	60	39	06	10	0	22	16	14	C
1788.01	hort	B	E	E	I	L	50	35	10	15	0	14	11	20	C
2400.01	hort	B	C	C	E	M	66	49	20	19	0	28	18	26	F

catalog number	15*	Scores 1	2	3	4	5	6	7	8	9	10	11	12	13	14
0071.14	hort	B	E	D	K	L	55	41	19	19	0	21	15	35	Q
2245.02	hort	A	E	D	I	L	52	52	29	26	N	42	26	27	Q
0071.02	hort	B	E	D	K	L	63	44	21	22	0	23	12	18	P
0071.01	hort	B	E	G	K	L	67	49	14	19	N	32	11	19	P
2245.01	hort	B	E	G	J	M	76	48	25	20	N	16	21	25	P
2325.09	hort	B	G	F	J	L	51	36	16	16	N	36	16	30	Q
2325.01	hort	B	G	F	J	M	77	44	24	22	N	43	20	36	Q
2731.02	hort	B	F	G	I	L	57	37	17	17	0	23	08	06	Q
1805.01	hort	B	H	G	J	L	62	38	20	18	0	20	13	30	Q
0103.01	dist	A	E	F	K	L	49	31	19	14	0	08	14	15	P
0201.01	hort	B	H	G	K	L	70	40	18	20	0	16	14	31	Q
0201.03	hort	B	H	G	K	M	73	53	19	15	0	18	10	32	P
2401.06	hort	B	G	H	J	M	51	36	17	21	0	17	11	10	P
2281.01	hort	A	C	F	K	L	48	42	10	11	0	11	19	35	P
2641.01	hort	B	C	F	I	L	49	35	11	13	N	15	11	13	P
0201.04	hort	B	E	F	J	M	55	39	19	15	0	12	16	32	P
2325.04	hort	B	C	G	J	M	73	45	17	24	N	08	14	18	P
2325.06	hort	B	C	F	J	M	70	41	20	22	0	09	16	20	P
2325.08	hort	B	C	F	J	L	69	37	15	19	0	13	09	17	P
0875.01	hort	B	C	F	K	M	60	39	18	18	N	08	10	09	Q
1730.01	hort	B	E	G	K	L	56	29	12	13	0	10	10	19	P
0870.01	hort	B	E	G	I	M	77	40	13	15	0	12	11	09	Q
0490.01	hort	B	H	F	K	L	49	30	15	14	0	12	10	10	P
0490.03	hort	B	H	F	K	L	49	34	13	16	0	14	10	16	P
0673.01	hort	A	H	F	K	M	70	42	25	21	0	15	16	19	P
0673.02	hort	A	H	G	K	L	58	41	19	17	0	13	11	17	Q
2722.01	hort	B	E	F	I	L	81	50	20	17	N	09	11	09	Q
3145.02	hort	B	H	F	I	L	48	31	06	09	0	07	10	08	Q
2230.01	hort	B	E	H	K	L	61	39	18	18	0	11	08	08	P
2171.01	hort	B	G	F	I	L	62	36	13	16	0	13	12	14	P
1775.01	hort	B	G	H	K	M	42	31	15	10	0	05	05	09	P
1780.01	hort	B	G	H	K	L	57	41	19	25	0	20	11	15	Q
2373.01	hort	A	G	H	K	L	61	44	15	13	0	09	15	19	Q
1835.01	hort	A	G	H	K	M	65	42	16	14	0	08	13	08	Q
2639.01	hort	A	G	F	K	M	53	34	13	17	0	13	07	22	Q
2357.01	hort	B	G	H	I	M	55	44	18	20	0	15	15	42	Q
2518.02	hort	A	G	H	I	L	55	34	13	15	0	08	06	09	Q
2518.01	hort	B	G	H	I	L	41	26	06	13	0	15	07	20	Q
2363.01	hort	B	G	H	J	M	61	42	19	21	0	09	18	48	Q
1810.01	hort	A	G	H	K	L	62	43	21	20	0	08	15	09	Q
0626.01	hort	B	G	H	I	L	51	42	20	20	0	10	10	13	Q
2402.02	hort	B	G	H	I	L	47	37	14	10	0	07	05	11	P
2402.01	hort	B	G	F	K	L	53	33	10	12	0	07	13	16	P
0652.01	hort	A	F	F	K	M	66	43	25	23	N	15	11	16	P
0652.02	hort	A	F	F	K	L	65	48	22	18	0	07	13	12	P
1630.01	hort	B	F	F	K	M	65	43	24	21	0	16	15	18	P
1661.01	hort	B	F	F	I	L	59	32	17	15	0	09	12	12	Q
1792.01	hort	B	F	F	J	M	71	39	23	15	N	11	13	27	Q
2557.01	hort	B	G	F	I	L	59	39	15	21	N	23	13	22	Q
2565.01	hort	A	G	G	K	L	50	30	10	10	0	06	08	26	Q
0666.01	hort	B	G	G	K	L	70	48	21	14	0	09	11	33	Q
0673.03	hort	B	H	F	I	M	80	52	30	25	0	12	11	13	Q
0664.01	hort	B	H	G	I	L	61	44	19	13	0	09	10	26	Q
0540.02	hort	B	G	G	I	L	62	40	12	15	N	09	13	09	P
0540.01	hort	B	H	G	I	L	55	41	11	07	N	10	16	09	Q
1052.01	hort	B	G	F	I	L	61	42	17	20	0	08	05	07	Q
2371.01	hort	B	G	G	K	L	55	38	15	15	0	15	12	16	Q
2239.09	hort	B	G	G	K	M	59	35	10	12	0	07	13	26	P
2239.13	hort	B	H	G	K	L	58	34	12	08	0	10	14	23	P
2542.01	hort	B	H	G	I	L	60	43	20	16	0	15	16	25	Q
2542.02	hort	B	H	G	I	L	47	37	13	14	0	12	13	22	Q

Abbreviations: A = light; B = dark; C = parallel; D = divergent; E = convergent; F = over pneumostome; G = above pneumostome; H = interrupted by pneumostome; I = above middle; J = under middle; K = in the middle; L = distinct; M = marginal; N = pigmentation present; O = pigmentation absent; P = thickening present; Q = thickening absent.

*The determinations are based on character 15 (type of ES). Note that the initial misidentifications mentioned in the text have been corrected.

Measurements were taken with a vernier calliper. The three considered parts in the oviduct usually were easily recognizable. The eversible portion has a slender, wrinkled appearance, whereas the firm portion is completely smooth. The latter also bears the retractor muscle. The boundary between the firm portion and the distal channel is marked by a more or less conspicuous constriction (Fig. 3). Individuals with an everted oviduct were not used for the measurements.

The scores were studied statistically with a canonical variate analysis (CVA) and a principal component analysis (PCA). Therefore the qualitative characters were encoded. Character 16 (type of ES) was not included in the calculations because we used it for the determinations, since Davies (1977, 1979) considered it as the most reliable one to distinguish the two or three species. As we will point out, it was not always easy to interpret this structure, so other good distinguishing characters were sought.

Calculations were performed with a Tektronix desk computer. For the concepts of CVA and PCA and the mathematical background involved, we refer to Seal (1964), Blackith & Reyment (1971) and Clifford & Stephenson (1975).

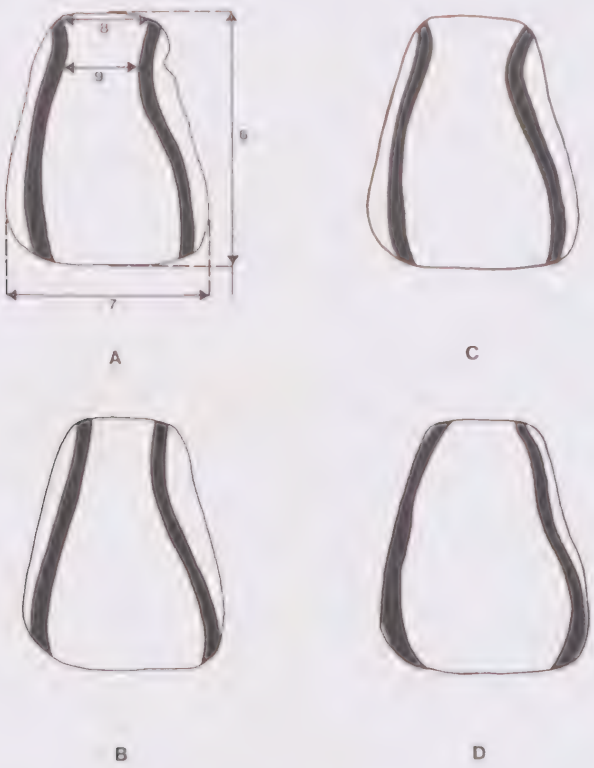

FIG. 1. Features of the mantle. **A,** Measurements taken on the mantle; the numbers refer to the character numbers used in the text, i.e., 6 = length of the mantle, 7 = breadth of the mantle, 8 = distance between the mantle bands on the head side, and 9 = the same measurement, but near the pneumostome; **B,** mantle bands parallel; **C,** mantle bands convergent; **D,** mantle bands divergent.

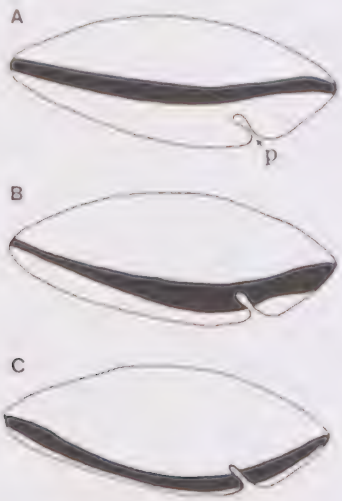

FIG. 2. Position of the mantle bands in regard to the pneumostome (P). **A,** Above the pneumostome; **B,** over the pneumostome; **C,** through the pneumostome.

The material currently is kept at the Rijksuniversitair Centrum Antwerpen, Laboratorium voor Algemene Dierkunde. Catalog numbers are given in Table 1. The specimens will be deposited later in the collections of the Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels.

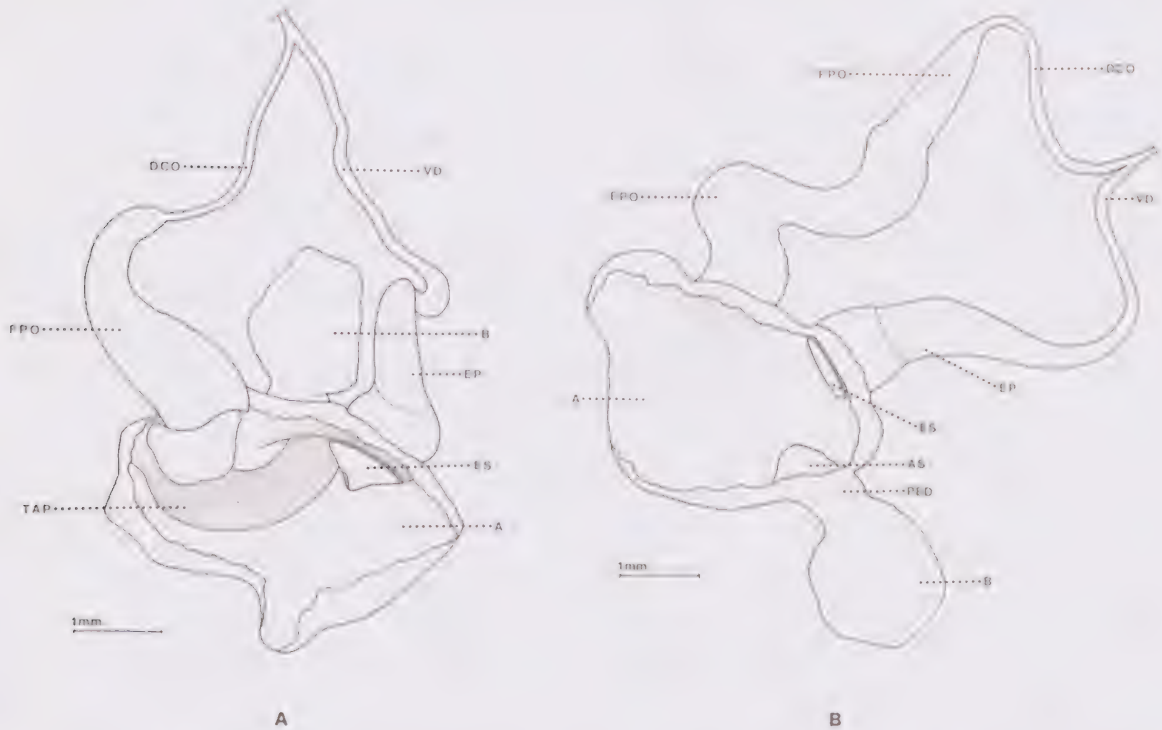

FIG. 3. Proximal parts of the genitalia of *Arion hortensis* s.l. The atria have been opened to show their internal structures. **A**, *A. distinctus* with partially everted oviduct (from Kessel); **B**, *A. hortensis* s.s. (from Dinant, Fonds de Leffe).

Abbreviations: A = atrium; AS = attachment site for the spermatophore; B = bursa; DCO = distal channel of the oviduct; EP = epiphallus; EPO = eversible portion of the oviduct; ES = structure associated with the outlet of the epiphallus; FPO = firm portion of the oviduct; GE = gutter leading into the epiphallus; PED = pedunculus; PM = papillate membrane in the epiphallus; TAP = thickening in the atrium near the entrance of the pedunculus; VD = vas deferens.

RESULTS

Variability of the individual characters

The data for each specimen are presented in Table 1. In the assumption that *Arion hortensis* s.l. comprises three species (Davies, 1977, 1979), we expected to find three types of ES in our material. However, we recognized only two types, corresponding with those of *A. distinctus* and *A. hortensis* s.s. (Fig. 4). Of a total of 346 specimens examined, 123 belonged to *A. hortensis* s.s. and the remaining 223 individuals were considered to be *A. distinctus*.

Tables 2 and 3 demonstrate that both qualitative and measured data show a great interspecific overlapping and, except perhaps for character 11 (the length of the eversible portion in the oviduct), none seems to be restricted to one of the species. Nevertheless, with some qualitative features there is a tendency to segregate both species. This is apparent for the body color, the position of the mantle band around the pneumostome and the thickening in the atrium. However, these features can only lead to preliminary identification, since even in the best case (position of the mantle band around the pneumostome) 15.6% of the specimens still would be wrongly identified. This figure amounts to 20.8% and 21.4%, respectively, for the thickening in the atrium and the body color. The other qualitative characters show no clear differences between both species (Table 2). Hence they have no importance for diagnostic purposes. The same applies to the measurements on the mantle (Fig. 1, Table

TABLE 2. Distribution of the qualitative characters among the material studied.

Character numbers and scores*		Species of *Arion*			
		A. distinctus		*A. hortensis* s.s.	
Character number	Score	Number of individuals	%	Number of individuals	%
1	A	169	75.8	20	16.3
	B	54	24.2	103	83.7
2	C	145	65.0	76	61.8
	D	14	6.3	32	26.0
	E	64	28.7	15	12.2
3	F	184	82.5	32	26.0
	G	22	9.9	91	74.0
	H	17	7.6	–	–
4	I	59	26.5	36	29.2
	J	54	24.2	27	22.0
	K	110	49.3	60	48.8
5	L	144	64.6	82	66.7
	M	79	35.4	41	33.3
10	N	215	96.4	100	81.3
	O	8	3.6	23	18.7
14	P	183	82.1	32	26.0
	Q	40	17.9	91	74.0

*The character numbers are the same as used in the text. The scores are explained in Table 1.

3). The measurements on the oviduct, however, seem different for the two species. Especially the length of the eversible portion appears as a possible diagnostic feature. Its strikingly high coefficient of variation (Table 3) is the result of some errors in the determinations of *Arion distinctus*. These will be discussed in the next section.

Canonical variate analysis (CVA)

In agreement with Davies (1977, 1979), some data in Tables 2 and 3 suggest that *Arion distinctus* and *A. hortensis* s.s. may constitute two morphologically different groups. In order to evaluate the extent to which both of these groups can be separated with the mentioned features, we performed a CVA on 14 of the 15 characters (the ES was used for the determinations). The result is illustrated in Fig. 5 as the frequency distribution of the first and only canonical variate in each species. The clear separation of both groups is due to differences in the eversible portion in the oviduct. Apparently, this feature is highly diagnostic. In fact, it turns out that specimens considered as *A. distinctus* always lack an eversible portion in the oviduct, whereas slugs identified as *A. hortensis* s.s. always have one (Fig. 3). In

TABLE 3. Mean values and coefficients of variation (in parentheses) of the measured data.

Character number	Slug species	
	Arion distinctus	*Arion hortensis* s.s.
6*	57.687** (16.386)	59.328 (16.144)
7	37.361 (14.120)	40.845 (14.445)
8	14.365 (31.020)	17.491 (28.286)
9	19.722 (25.698)	17.517 (27.097)
11	1.326 (377.500)	25.086 (31.693)
12	22.291 (32.017)	13.328 (34.174)
13	29.657 (29.581)	23.431 (43.546)

*The character numbers are the same as used in the text.
**The mean values are given in 0.1 mm.

the latter group, however, some individuals show an ES which is somewhat bent, resembling in this way *A. distinctus*. These specimens constitute the small region of overlapping in Fig. 5. They are also responsible for the high coefficient of variation in *A. distinctus* (Table 3). The misidentifications were made because Davies (1977, 1979) reported two genitalial forms in British *A. distinctus*: one having a clear eversible portion in the oviduct and one without such portion. Clearly, the former might be confused with *A. hortensis* s.s. But, after a re-examination of the ES in both species, we found that the bent forms, which also show an eversible portion in their oviduct, actually should be referred to *A. hortensis* s.s. and not to the first genitalial form of *A. distinctus*.

In order to avoid further confusion, we have defined the ES as follows. The ES of *Arion distinctus* is a conspicuous, somewhat flattened cone, covering the entire outlet of the epiphallus (Fig. 4). This cone surrounds a narrow gutter leading into the central channel of the epiphallus. Although the cone is usually rather prominent, it sometimes can be nearly flat.

In *Arion hortensis* s.s. (Fig. 4), the ES differs from the foregoing in several ways. It is much less conspicuous and it can easily be overlooked. Usually, it is a straight oblong plate, which never covers the entire outlet of the epiphallus. Although it can be curved to some degree (e.g., the bent forms mentioned above), it does not form the typical gutter as seen in *A. distinctus*. Hence, under and alongside the ES one usually can observe the papillate

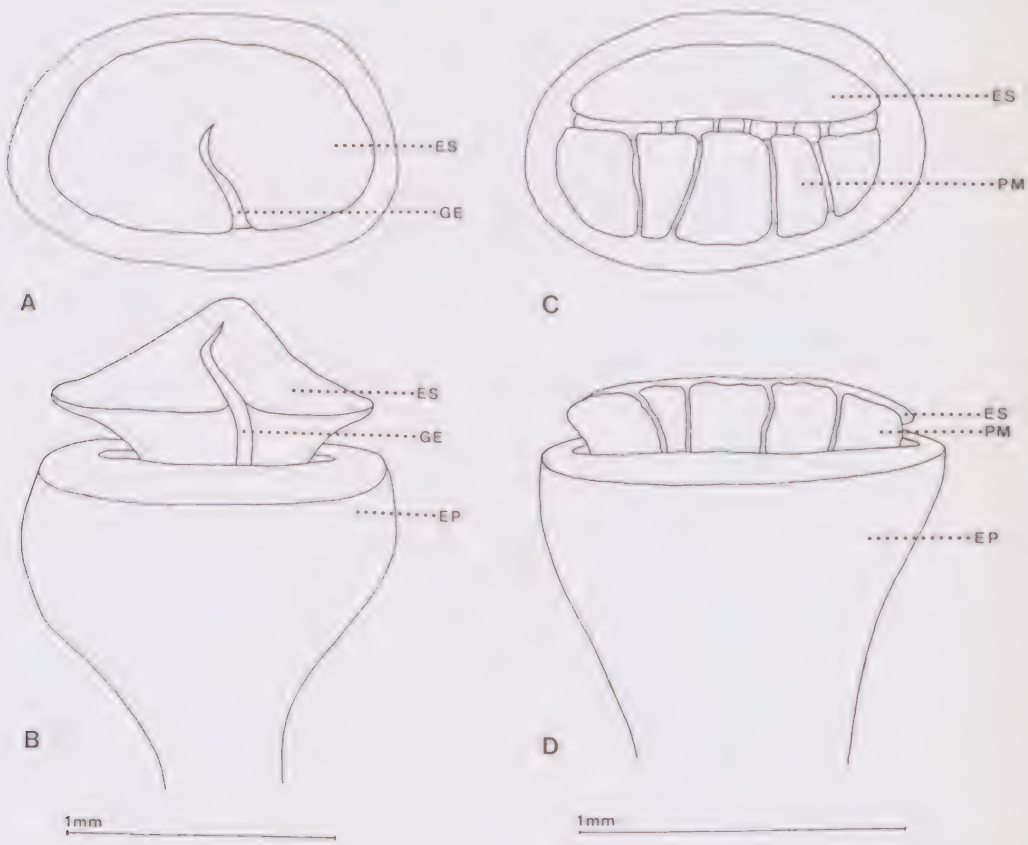

FIG. 4. Structure associated with the outlet of the epiphallus. **A, B,** *Arion distinctus* (from Temse); A = seen from above, B = lateral view. **C, D,** *A. hortensis* s.s. (from Dinant, Fonds de Leffe); C = seen from above, D = lateral view. For abbreviations, see Fig. 3.

membrane in the central channel of the epiphallus. This membrane is visible in *A. distinctus* only after pulling of the ES, or after dissecting the epiphallus.

Principal component analysis (PCA)

Since the CVA indicates that the presence or absence of an eversible portion in the oviduct is of high diagnostic value in the Belgian material, we thought that it would be interesting to investigate whether it is still possible to distinguish the two species with only the remaining 13 characters. Here we regard both groups as one homogeneous entity in which we search for possible subdivisions corresponding with the two species defined on their ES and the presence/absence of an eversible portion in the oviduct.

In order to resolve this question, three PCAs were performed: one in which all the 13 characters were treated together, one in which only the seven qualitative features were used, and one in which we analyzed the six measurements. In Table 4, the percentages of variance for each axis in the three PCAs are given. We will consider, however, only the first three principal components since they canalize most of the variation and since they are the only ones to reveal interpretable specimen groupings.

Only the PCA on the 13 characters gives a more or less clear result, as shown in Fig. 6. Inspection of this graph demonstrates that a fairly good segregation of the two species is achieved along the second principal component. This axis shows a positive correlation with

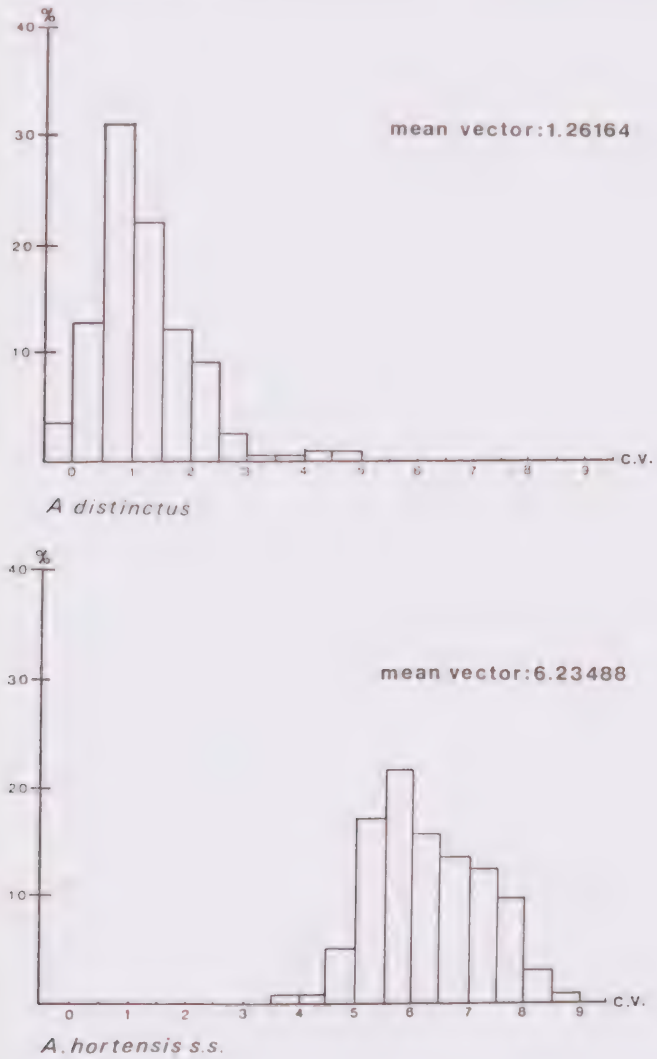

FIG. 5. Canonical Variate Analysis on 14 characters. The canonical variates are grouped into classes of 0.5 units (abscissa).

the length of the firm portion in the oviduct (0.664) and with the length of its distal channel (0.547). There is a negative correlation with the thickening in the atrium (-0.647), the body color (-0.620) and the path of the lateral band around the pneumostome (-0.517). The correlations between the 13 variables and the first three principal components in this analysis are summarized in Table 5.

With a PCA on the seven qualitative features, no clear separation of the two species is observed, but with a PCA on the six measurements a slight segregation along the second axis is visible. We find a correlation with the length of the firm portion in the oviduct (0.849) and the length of the distal channel (0.707). The segregation induced by the six measurements, however, is much less obvious than that resulting from the analysis of the 13 characters together.

From the PCA, it is clear that in Belgium none of the characters we studied (other than the ES and the eversible portion in the oviduct) can be relied on to distinguish *Arion hortensis* s.s. from *A. distinctus*. Nevertheless, two qualitative characters, the body color and

TABLE 4. Percent contribution of each principal component (axis) to the total variance in the analyses on 13, 7 and 6 characters, respectively.

Principal component	% Variance		
	13	7	6
1	20.47	24.02	43.43
2	16.65	17.68	22.52
3	10.91	13.95	11.98
4	7.71	12.70	9.87
5	7.02	11.68	6.60
6	6.70	11.11	5.60
7	6.49	8.69	
8	5.67		
9	5.16		
10	4.33		
11	3.91		
12	2.71		
13	2.28		

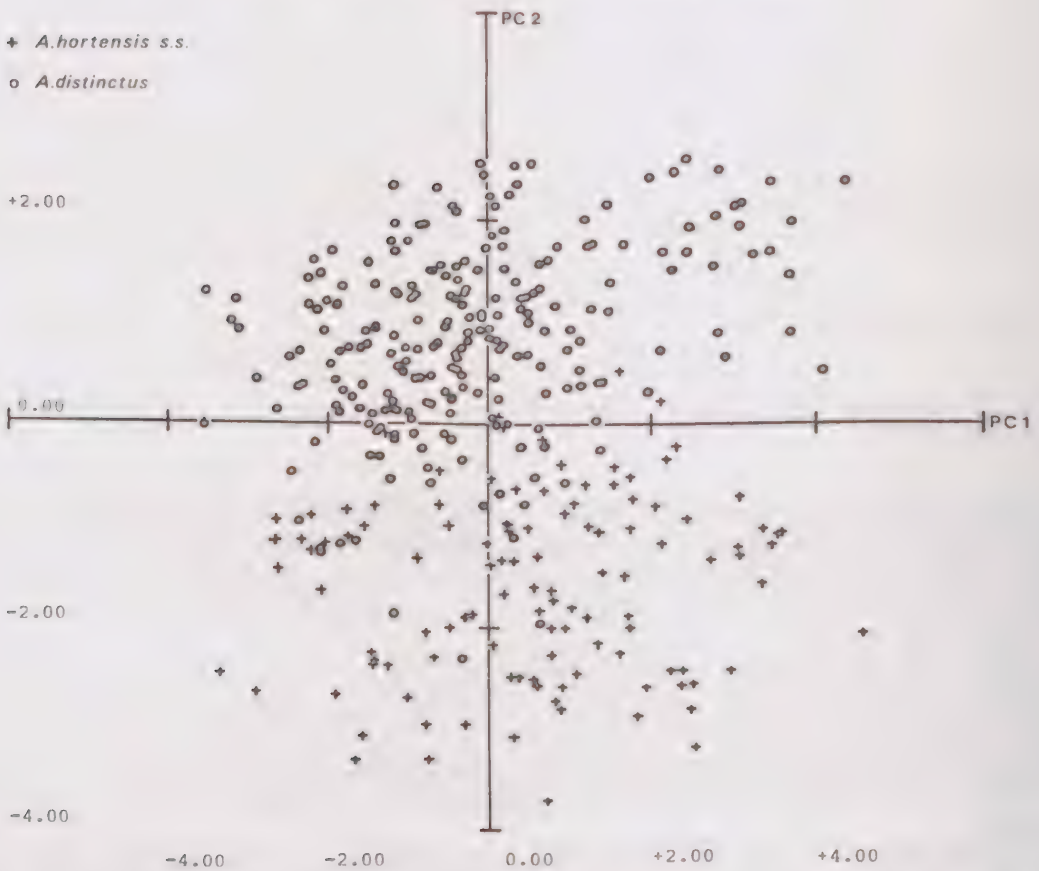

FIG. 6. Principal Component Analysis of 13 characters using the first and second principal components (axes).

TABLE 5. Correlations between the characters and the first three principal components in the analysis on the 13 features.

Character number	Correlations		
	1	2	3
1*	0.193	-0.620	0.133
2	0.129	0.124	0.622
3	0.110	-0.517	-0.025
4	-0.121	0.082	-0.620
5	0.076	0.099	-0.561
6	0.795	0.096	0.036
7	0.852	-0.133	0.112
8	0.769	-0.100	-0.332
9	0.722	0.356	-0.164
10	0.192	-0.398	0.127
12**	0.095	0.664	0.275
13	0.206	0.547	0.205
14	0.124	-0.647	0.168

*The character numbers are the same as used in the text.

**Note that character 11 has been omitted.

the path of the lateral band around the pneumostome, may be indicative during field work. Such field determinations, however, always need to be checked by dissection of the genitalia. A combination of measured and qualitative features makes a distinction between both species quite possible as demonstrated by the PCA on the 13 variables (Fig. 6).

Conclusions

This study shows that in Belgium *Arion distinctus* differs from *A. hortensis* s.s. in having no eversible portion in the oviduct (Fig. 3A) and in having a conical-shaped ES covering the entire outlet of the epiphallus. This ES also typically forms a gutter leading into the epiphallus (Fig. 4A,B). In addition, the firm portion, and the distal channel in the oviduct as well, are relatively longer than in *A. hortensis* s.s. Moreover, in *A. distinctus* the inner side of the atrium is more thickened (Fig. 3A). Externally, the species is usually lighter in color, which varies from gray to brownish, and its lateral band generally runs over the pneumostome (Fig. 2B,C). *A. hortensis* s.s. has a very dark blue to black color and its lateral band usually runs more above the pneumostome (Fig. 2A). Internally, the species is characterized by the presence of a conspicuous eversible portion in its oviduct (Fig. 3B) and by the relatively inconspicuous, more or less straight, oblong ES, which does not cover the entire outlet of the epiphallus and which does not form a gutter leading into it (Fig. 4C,D).

DISCUSSION

In general, our results agree well with those of Davies (1977, 1979) and De Wilde (1983). However, since we found *Arion distinctus* to be characterized by the absence of an eversible portion in its oviduct, it seems as if the genitalial dimorphism in this species (Davies, 1977,

1979) does not exist among the Belgian material. This is surprising because in Great Britain *A. distinctus* with an eversible portion in the oviduct occurs nearly half as frequently as does *A. distinctus* without an eversible portion (Davies, 1977). In Belgium only the latter was found (Backeljau, 1981; De Wilde, 1983). Also, we could detect only *A. distinctus* without an eversible portion in the oviduct among specimens collected in Tromsø (northern Norway) (Backeljau et al., 1983). The significance of the apparent dimorphism in the oviduct of *A. distinctus* needs further study, since it partially can rule out the diagnostic value of the presence/absence of the eversible portion.

De Winter (in litt.) found in The Netherlands specimens which could belong to *Arion distinctus*, although they have an eversible portion. This material, however, was identified by Davies as *A. hortensis* s.s.; until we have seen it we cannot exclude the possibility of *A. distinctus*, considering the above-mentioned dimorphism.

Consquently, we are inclined to state that (in Belgium at least) the absence of an eversible portion in the oviduct is characteristic of *Arion distinctus*, whereas its presence indicates *A. hortensis* s.s. However, we do not follow De Wilde (1983) in generalizing this observation, because we are convinced that it does not hold for the whole geographical range of *A. hortensis* s.l.

Davies (1977, 1979) supplemented her morphological data with observations on the spermatophores and mating behaviour of the different forms in the complex. Our material contained 25 spermatophores of *Arion hortensis* s.s. and four of *A. distinctus* (Fig. 7). They were all found in the atria of recipient individuals and they correspond with the respective genitalial features. So *hortensis*-like spermatophores were found only in *hortensis*-like genitalia, whereas the *distinctus*-like spermatophores were noted only in *distinctus*-like genitalia. In this respect, the spermatophores and the corresponding genitalia agree perfectly well with the descriptions of Davies (1977, 1979).

Although the differences between spermatophores in the two species may be somewhat subtle and although one might suspect that certain differences may be the result of the digestion process going on in the recipient genitalia, we are convinced that at least the serrated ridge on the spermatophores of *Arion hortensis* s.s. (Fig. 7) is a reliable discriminating feature, since it is lacking in *A. distinctus*. The absence of this ridge can hardly be caused by the digestion process because we found the remains of completely disintegrated spermatophores which still showed the serration in the bursae of several *A. hortensis* s.s. Detailed descriptions of the spermatophores are given by Davies (1977, 1979).

Since *Arion distinctus* and *A. hortensis* s.s. commonly occur in mixed populations and in view of the differences in the genitalia, spermatophores and mating behavior, we follow Davies (1979) and De Wilde (1983) in considering both forms as morphologically different groups. An electrophoretic survey is now in progress, in order to demonstrate whether or not these forms constitute genetically isolated populations which might be regarded as biological species (Backeljau, 1985a,b).

As stated by Davies (1977, 1979) and De Wilde (1983), the occurrence of *Arion hortensis* s.s. needs confirmation in large parts of its supposed geographical range. In fact, several previous authors figured *A. distinctus* under the name *A. hortensis*. However, drawings should be interpreted very carefully since the discriminating features of the oviduct or the epiphallus will not be apparent unless the author paid special attention to them. Consequently, illustrations of previous authors should be taken with caution.

Preliminary distribution maps of the species complex in Belgium are given by Backeljau (1981) and De Wilde (1983). The third proposed species, *Arion owenii*, is not known to occur in Belgium.

Concerning the methods we used, it can be argued that we used measurements on soft organs, which after preservation may shrink in various ways. It cannot be denied that this causes inevitable errors. However, since each specimen has undergone the same treatment,

FIG. 7. Spermatophores. **A**, *Arion distinctus* (from Temse); **B**, *A. hortensis* s.s. (from Boirs). Note the serrated ridge on the spermatophores of *A. hortensis* s.s.

it may be assumed that the effects of shrinkage are more or less the same in all individuals. Hence, we do not think that the errors affect the interpretation of our data in a decisive way. Of course, it is very likely that, if someone else were to perform our analyses, he/she would probably find different values, but the general tendencies and interpretations undoubtedly would be the same as ours. Finally, one also could suggest that it would have been better to use ratios (e.g., length/breadth) instead of the separate measurements. Ratios, however, do not avoid the mentioned errors. On the contrary, they may even introduce new errors caused, for instance, by allometric growth. A much more profound discussion on the disadvantages of ratios in studies such as ours is given in Blackith & Reyment (1971). A further rationale on multivariate statistics is given by Clifford & Stephenson (1975).

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A CYTOTAXONOMIC STUDY OF SOME SPANISH AND PORTUGUESE HELICIDAE (PULMONATA: GEOPHILA)

M.A. Ramos and M.T. Aparicio

ABSTRACT

Eleven species of land snails belonging to four subfamilies of the family Helicidae from Spain and Portugal have chromosome numbers ranging from n = 21/2n = 42 to n = 30/2n = 60. These chromosome numbers are within the range already known for this family. Eighty-eight species of the Helicidae have now been studied cytologically.

Three of the species investigated here, *Helicella ordunensis, H. stiparum* and *Oestophora barbula*, show a clear band in the largest bivalent. This band is thought to be similar to that of other species previously studied. These common characteristics suggest that the clear band is an ancestral condition for the family.

INTRODUCTION

Recent papers (Aparicio, 1981, 1983; Ramos, 1982) have increased the number of helicid snails cytologically studied to 81 species. Yet, there is no major hypothesis about the karyotypic evolution of this family, mainly because the available results are not very conclusive and also because phylogenetic relationships based on comparative morphology have not been established (Aparicio, 1983).

Our present data increase the knowledge on cytotaxonomy of the Helicidae by adding 11 Spanish and Portuguese species to those studied. Four of these 11 species had been investigated by previous authors.

MATERIALS AND METHODS

The 11 species studied here were collected in the Iberian Peninsula, with the exception of *Theba pisana*, which was collected in the Canary Islands. The species are listed in Table 1, as well as the Universal Transverse Mercator (U.T.M.) grid coordinates of the localities sampled.

Determinations have been made by the authors, considering both conchological and genital characters, following the nomenclature proposed by Gittenberger et al. (1970). Voucher specimens have been deposited in the Museo Nacional de Ciencias Naturales, Madrid, Spain.

Observations were made on germ cells in the ovotestes. Gonial tissues were hypotonized with Ohnuki's modified solution, fixed with methanol- or ethanol-acetic acid, then stained with lacto-propionic orcein and squashed.

RESULTS

The results are summarized in Table 1.

Subfamily Helicellinae

Spermatogonial chromosomes are mostly metacentric and submetacentric, varying gradually in size, so we cannot distinguish groups of pairs. Two chiasmata are frequently found at diakinesis in the two largest bivalents; other bivalents usually show only one chiasma.

Helicella ordunensis (Kobelt 1883) has a diploid number of 2n = 52. The metacentric and submetacentric chromosomes increase gradually in size (Fig. 1) from 1.6 μm to 4.5 μm, as an average. In the specimens from Cañon del Rio Lobos (Soria), a constant clear band is seen in the largest bivalent at diakinesis and metaphase I cells (Fig. 2), being less conspicuous in the specimens from Quintanilla Escalada (Burgos).

TABLE 1. Chromosome numbers of 11 species of Helicidae from Spain and Portugal.

Species	n	2n	Localities	No. of individuals
Subfamily Helicellinae				
Helicella ordunensis	26	52	Quintanilla Escalada, Burgos (9-V-1982) 30TVN3739*	3
			Cañón del Río Lobos, Soria (30-X-1983) 30TVM9422	3
Helicella stiparum	25		Alcores de Punta Entinas, Almería (28-X-1982) 30SWF2162	5
Helicopsis (Xeromicra) apicina	26	52	Castillo de San Felipe, Setúbal, Portugal (20-X-1982)	4
*Candidula intersecta***	26		Castillo de San Felipe, Setúbal, Portugal (22-X-1982)	1
Subfamily Hygromiinae				
Hygromia limbata	21	42	Los Pandos, Santander (8-V-1982) 30TVN2673	1
			Santander, Cobanera city district, Santander (9-V-1982) 30TVP3513	3
*Trichia (Trichia) hispida***	23	46	Oña, Burgos (12-V-1982) 30TVN6633	5
Euomphalia (Mengoana) brigantina	26	52	Vidiago, Asturias (25-IV-1982) 30TUP6506	2
			Los Pandos, Santander (8-V-1982) 30TVN2673	2
Portugala inchoata	26		Castillo de San Felipe, Setúbal, Portugal (20-X-1982)	6
Subfamily Helicodontinae				
Oestophora (Oestophora) barbula	30	60	Castillo de San Felipe, Setúbal, Portugal (20-X-1982)	3
			Castillo de Palmela, Palmela, Portugal (22-X-1982)	2
			Embalse de Peñarrubia, León (11-X-1982) 29TPH7903	3
Subfamily Helicinae				
*Pseudotachea litturata***	22		Tarifa, Cádiz (26-X-1982) 30STE6390	1
*Theba pisana***	30	60	Tahiche, Lanzarote, Canarias (8-V-1981)	2
			Haria, Lanzarote, Canarias (8-V-1981)	2
			La Ampuyenta, Fuerteventura, Canarias (6-V-1981)	2

*U.T.M. grid coordinate.

**Species previously studied.

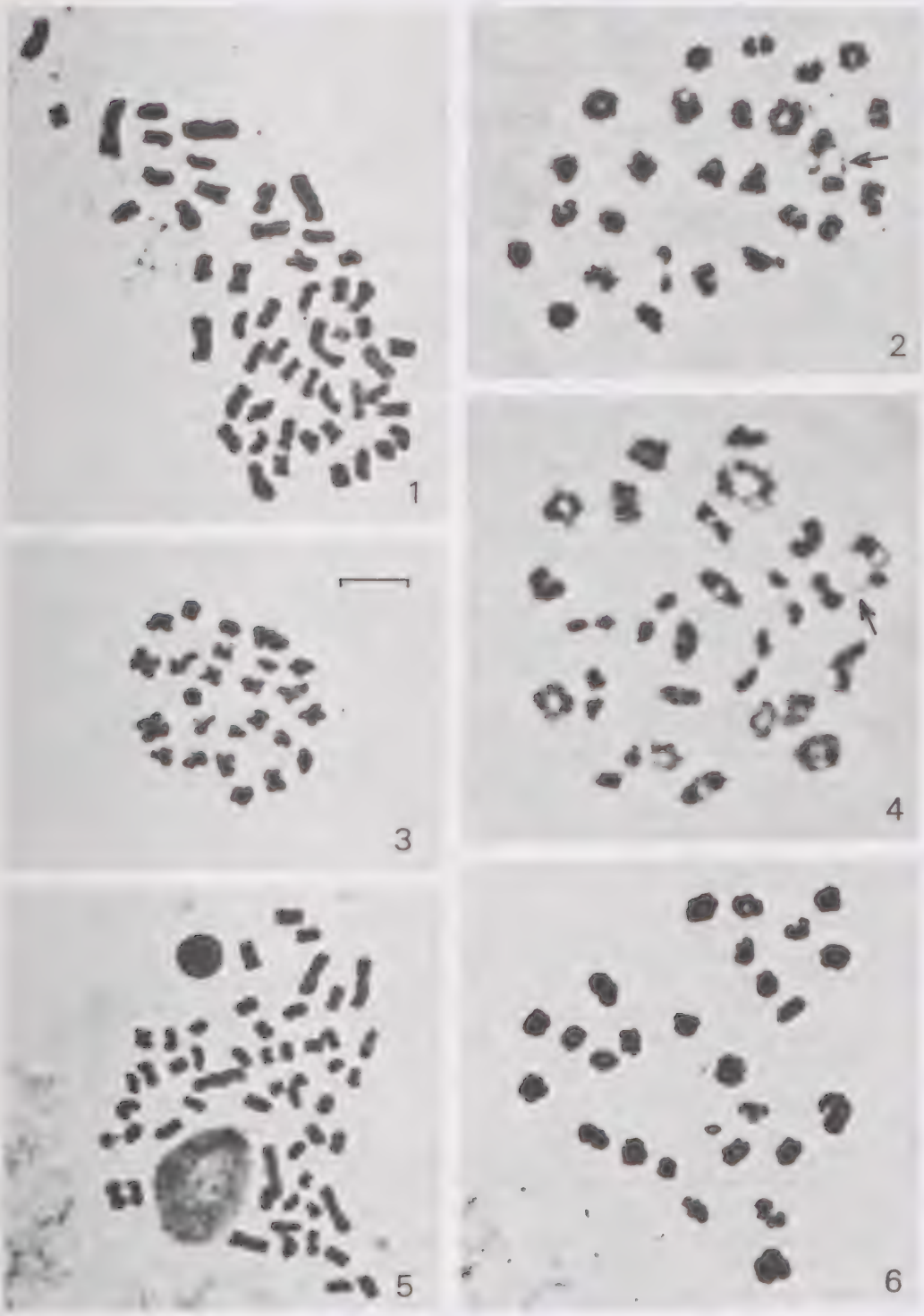


FIG. 1. *Helicella ordunensis*, spermatogonial metaphase, 2n = 52. FIG. 2. *H. ordunensis*, metaphase I, n = 26, the largest bivalent showing a clear band. FIG. 3. *H. stiparum*, metaphase II, n = 25. FIG. 4. *H. stiparum*, diakinesis, n = 25; the largest bivalent shows a clear band. FIG. 5. *Helicopsis apicina*, spermatogonial metaphase, 2n = 52. FIG. 6. *H. apicina*, metaphase I, n = 26. The bar represents 5 μm.

Helicella stiparum (Rossmässler 1854). The haploid chromosome number of this species is n = 25. At metaphase II (Fig. 3), chromosomes are metacentric and submetacentric. The largest bivalent shows a constant clear band at diakinesis and metaphase I cells (Fig. 4) similar to that one found in the above-mentioned species.

Helicopsis (Xeromicra) apicina (Lamarck 1822) has a karyotype with 52 chromosomes, of which two large pairs stand out. Both are submetacentric. One pair is 3.9 μm in size in full metaphase, while the other is 3.6 μm in size. The smallest pair is 1.4 μm (Fig. 5). The haploid chromosome number is n = 26 (Fig. 6).

Candidula intersecta (Poizet 1801) has an haploid chromosome number of n = 26 (Fig. 7).

Subfamily Hygromiinae

Hygromia limbata (Draparnaud 1805) has 42 spermatogonial chromosomes, of which three pairs are larger and identifiable (Fig. 8). The two largest ones are metacentric and their sizes are 5.2 μm and 4.5 μm, respectively. The third one is a submetacentric pair of 4.1 μm. The smallest pair is 1.7 μm. The haploid number is n = 21 (Fig. 9). In diakinesis and metaphase I cells, bivalents are frequently cross-shaped, rods being rare.

Trichia (Trichia) hispida (Linnaeus 1758). The diploid number of this species is 2n = 46 (Fig. 10). The largest metacentric pair is 5.9 μm in size; the following pair is also metacentric and 5.3 μm in size; the smallest one is 2.1 μm. First meiotic divisions have 23 bivalents (Fig. 11); one chiasma per bivalent is observed, except for the three largest ones which frequently show two chiasmata.

Euomphalia (Mengoana) brigantina (Da Silva Mengo 1867) has 2n = 52 metacentric and submetacentric chromosomes. One pair, which is 4.9 μm in size, is the largest one of a decreasing series that ends with a pair of about 2 μm (Fig. 12). The haploid chromosome number is n = 26 (Fig. 13).

Portugala inchoata (Morelet 1845) has a diploid number of 2n = 52 (Fig. 14). The chromosome size ranges between 4.2 μm and 1.3 μm. The haploid number is n = 26 (Figs. 15, 16). Spermatogonial as well as metaphase II chromosomes are mostly metacentric and submetacentric. Two chiasmata are usually found at diakinesis in the two largest pairs and only one in the other bivalents (Fig. 16).

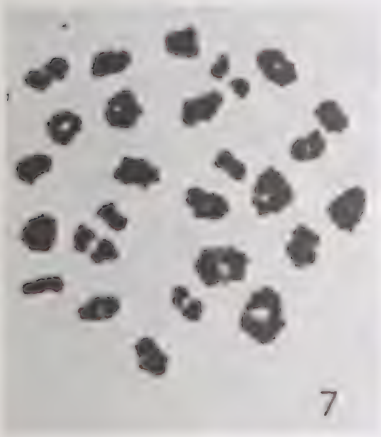
Subfamily Helicodontinae

Oestophora (Oestophora) barbula (Rossmässler 1838). The diploid number is 2n = 60 (Fig. 17). The chromosome size at full metaphase ranges among 4.5 μm for the largest pair, 3.9 μm for the next pair and 1.4 μm for the smallest pair. The haploid number is n = 30 (Fig. 18). In all the diakinesis and metaphase I cells, the largest bivalent shows a clear band wider but similar in shape and position to that found in the two species of the genus *Helicella* earlier described.

Subfamily Helicinae

Pseudotachea litturata (Pfeiffer 1851). The haploid chromosome number is n = 22 (Figs. 19, 20). The chromosomes are metacentric and submetacentric. This is the only species mentioned in this paper for which we can group chromosomes and distinguish a large metacentric pair (A group) whose size is about twice that of the next pair (B group). During diakinesis, all the bivalents usually form only one chiasma, except for the three largest pairs which often form two. The A pair shows three or four chiasmata in many cells.

FIG. 7. *Candidula intersecta*, metaphase I, n = 26. FIG. 8. *Hygromia limbata*, spermatogonial metaphase, 2n = 42. FIG. 9. *H. limbata*, metaphase I, n = 21. FIG. 10. *Trichia hispida*, spermatogonial metaphase, 2n = 46. FIG. 11. *T. hispida*, diakinesis, n = 23. FIG. 12. *Euomphalia brigantina*, spermatogonial metaphase, 2n = 52. FIG. 13. *E. brigantina*, diakinesis, n = 26. The bar represents 5 μm.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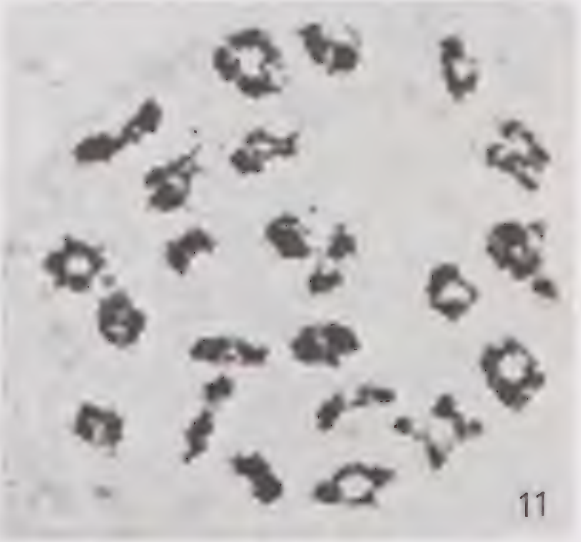
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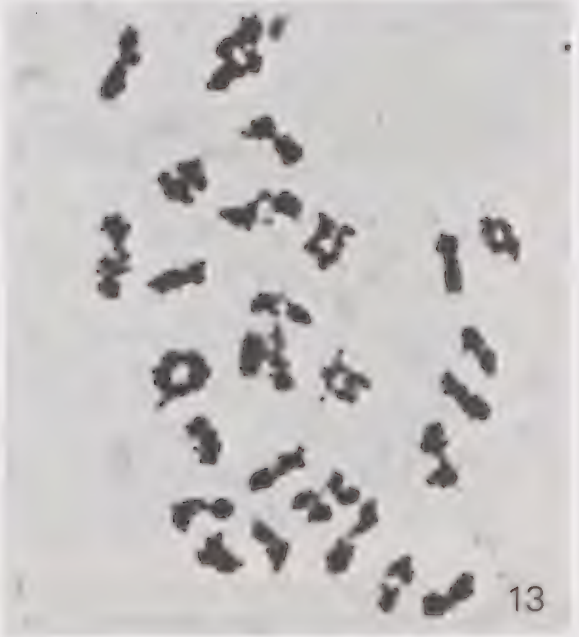
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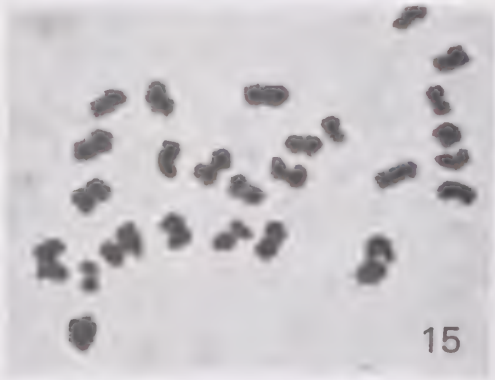

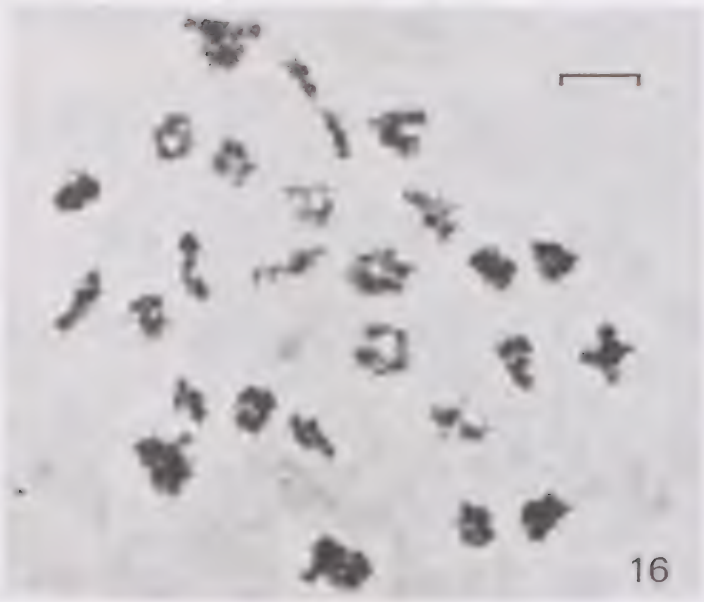

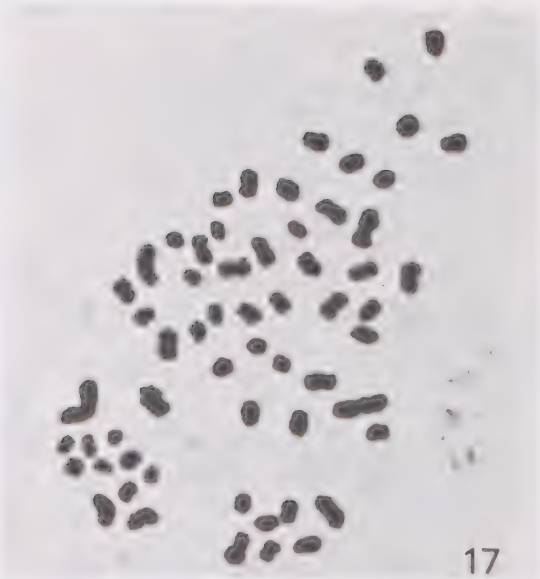

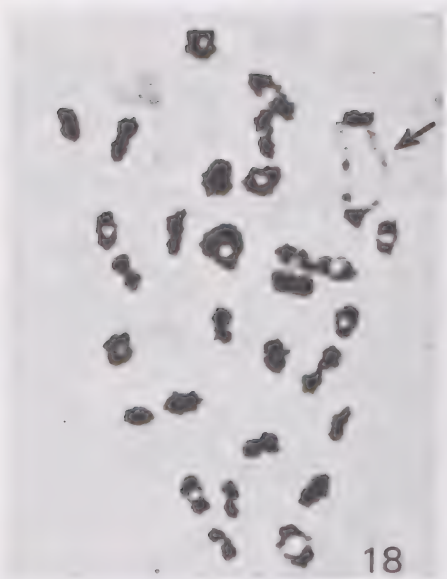

FIG. 14. *Portugala inchoata*, spermatogonial metaphase, 2n = 52. FIG. 15. *P. inchoata*, metaphase II, n = 26. FIG. 16. *P. inchoata*, diakinesis, n = 26. FIG. 17. *Oestophora barbula*, spermatogonial metaphase, 2n = 60. FIG. 18. *O. barbula*, metaphase I, n = 30, the largest bivalent showing a clear band. The bar represents 5 μm.

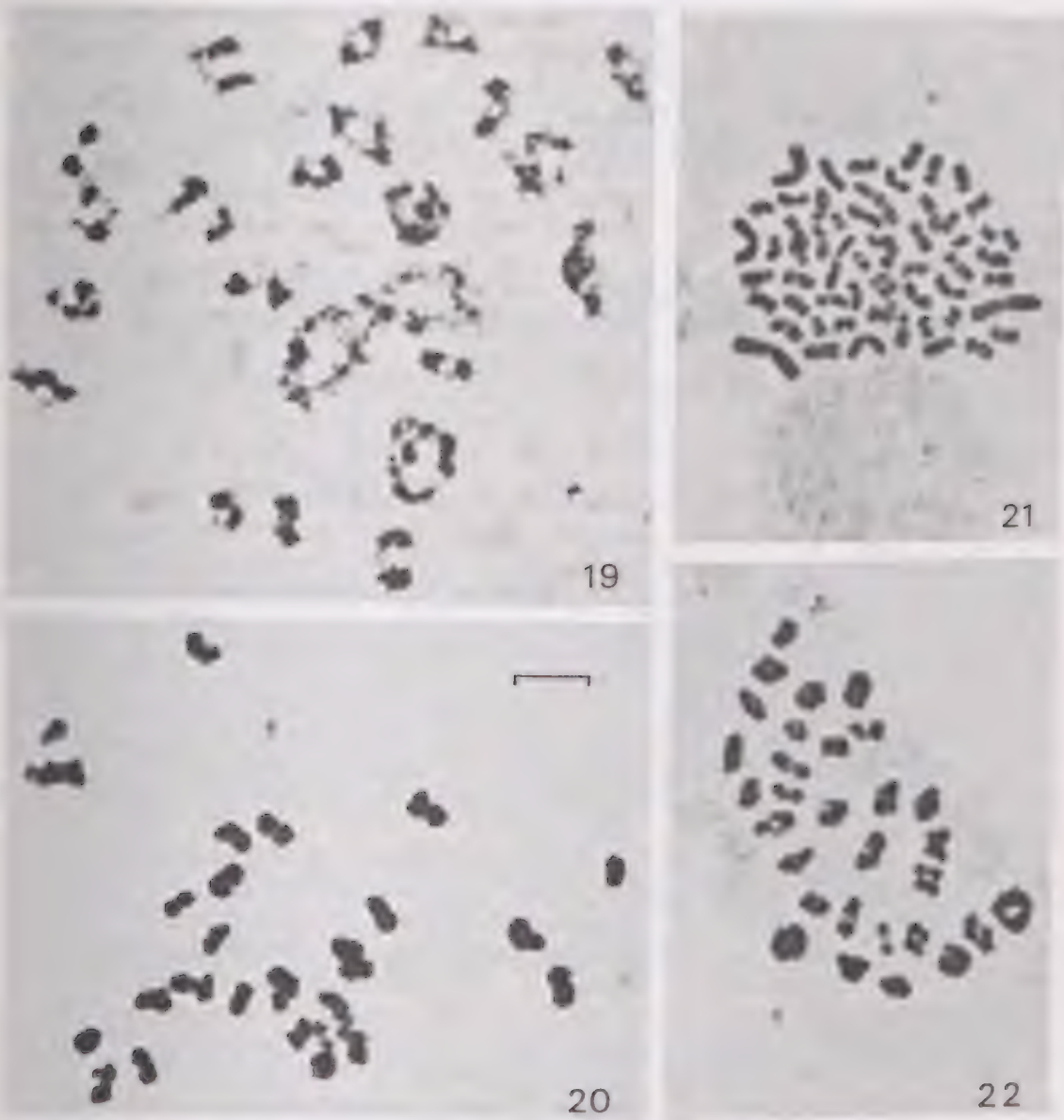

FIG. 19. *Pseudotachea litturata*, diakinesis, n = 22. FIG. 20. *P. litturata*, metaphase II, n = 22. FIG. 21. *Theba pisana*, spermatogonial metaphase, 2n = 60. FIG. 22. *T. pisana*, metaphase I, n = 30. The bar represents 5 μm.

Theba pisana (Müller 1774). The diploid number observed in this species is 2n = 60, the chromosomes being metacentric and submetacentric (Fig. 21). The two largest pairs (5.3 μm and 4.1 μm, respectively, in size) are metacentric and indistinguishable from the other 28 pairs, which form a series gradually decreasing to 1.4 μm. The haploid number is n = 30 (Fig. 22). We have observed one chiasma per bivalent and sometimes two in the largest bivalent.

DISCUSSION

Subfamily Helicellinae

The karyotypes of the two *Helicella* species studied in this paper are similar to the other

species of this genus previously studied. The most conspicuous character which they show is the clear band, which has the same structure as the clear band found in *Helicella itala* (Aparicio, 1981).

Helicella stiparum is the only species in which the chromosome number (n = 25) differs from that (n = 26) of all the other species of this genus already known (Perrot, 1938; Rainer, 1967; Aparicio, 1981). Such a difference is not surprising because of the morphological and ecological divergences between *H. stiparum* and the other *Helicella* species. *H. stiparum* has a peculiar solid and white shell and shows a very restricted distribution to a small area in southern Spain.

The only species studied cytologically in the genus *Helicopsis, H. (Xeromicra) apicina*, has a chromosome number (n = 26) which is coincident with the basic chromosome number of the subfamily Helicellinae.

The results of *Candidula intersecta* (n = 26) confirm those previously known (Butot & Kiauta, 1969).

Subfamily Hygromiinae

Hygromia limbata has the same chromosome number (n = 21) as that found in the only other species (*Hygromia cinctella*) studied in this genus, and has metaphase I bivalents similar to those figured by Perrot (1938) for *H. cinctella*, with two bivalents larger in size. These two pairs of chromosomes can be identified also in spermatogonial mitosis.

Euomphalia (Mengoana) brigantina has a different chromosome number (n = 26) from those found in the two species previously studied: *E. (Harmozica) arpatschaina* (n = 23; Rainer, 1967) and *E. (E.) strigella* (n = 24; Aparicio, 1981). These differences agree with the inclusion of the three species in three different subgenera. These results are also cytologically interesting because such an intrageneric variation is not common within helicid snails.

The number and shape of the bivalents (n = 23) of *Trichia hispida* described in this paper are similar to those figured by Mallet (1962) and Butot & Kiauta (1970), results which are confirmed by spermatogonial mitosis (2n = 46).

The genus *Portugala* was erected recently by Gittenberger (1980) to isolate the species *Helix inchoata* from the others of this subfamily. Gittenberger pointed out that *P. inchoata*: 1) comes close anatomically to the *Monachoides* species-group, 2) its dart structure resembles that of species of the subfamily Helicinae, and 3) it is related to the species of the genus *Hygromia* (in which it previously was included), though differing from them mostly in conchological characters. From a cytological point of view, the exclusion of the species from *Hygromia* and the new genus *Portugala* are justified, when taking into account the great differences between *P. inchoata* (n = 26) and the *Hygromia* species (n = 21). On the other hand, the chromosome number of *P. inchoata* is within the range of variation of the Helicinae (Table 2), and its shell polymorphism is convergent with species of *Cepaea* (Helicinae; Sacchi, 1981).

TABLE 2. Chromosome numbers of the family Helicidae.

Subfamily	No. of species	Haploid chromosome numbers										
		21	22	23	24	25	26	27	28	29	30	31
Helicellinae	19				1	5	11	2				
Cochlicellinae	2			2								
Monachinae	9			8	1							
Hygromiinae	16	2		9	2		3					
Helicodontinae	2							1			1	
Ariantinae	12									3	8	1
Helicinae	28		8			3	6	7			4	
Total	88	2	8	19	4	8	20	10	0	3	13	1

Subfamily Helicodontinae

The chromosome number of *Oestophora barbula* (n = 30) is quite different from *Helicodonta obvoluta* (n = 27), the single species cytologically known from the same subfamily. *O. barbula* shows a clear band in the largest bivalent, which has not been found in *H. obvoluta*. These differences are in accordance with the marked anatomical and conchological divergences between the two genera.

Subfamily Helicinae

Our results on *Pseudotachea litturata* (n = 22) confirm those of Perrot (1938). Chromosome morphology and number of chiasmata per bivalent are very similar to those of the other species of this subfamily with the same chromosome number, as would be expected from the close relationships between them (Aparicio, 1983).

Results on Canarian specimens of *Theba pisana* confirm the haploid chromosome number found in specimens from England (Mallet, 1962), Australia (Laws, 1965) and Spanish mainland populations (Aparicio, 1983). Spermatogonial mitoses had 60 chromosomes. All these results differ from those of Rainer (n = 28; 1967).

The clear band

The clear band is a negative-staining region described for the largest bivalent of *Cepaea nemoralis* (Ramos, 1980, 1982). A similar structure has been described for another helicine species, *Eobania vermiculata* (Aparicio, 1983), as well as for the helicelline *Helicella itala* (Aparicio, 1981). We also found it in two other species of Helicellinae, *H. ordunensis* and *H. stiparum*, and in a species of Helicodontinae, *Oestophora barbula*.

The clear band has common characters for all the species in which it has appeared: 1) it is present always in the largest bivalent; 2) it appears at diakinesis and metaphase I, but is not visible during mitosis or metaphase II; 3) it is interstitially located and includes the centromeric region (except in *Cepaea nemoralis*, where it is close to the centromeric region (Ramos, 1982)). These common characteristics suggest that the largest pair of chromosomes that carries the band is homologous in the six species in which the band has been found. If we additionally take into account that these species belong to three different subfamilies, it would seem that the clear band is an ancestral condition for the family. Differences in size of this large pair among the six species might be related to differences in their chromosome number.

On the other hand, the variability in the appearance of the clear band within and between specimens of *Cepaea nemoralis* (Ramos, 1982) and *Helicella itala* (Aparicio, 1981), and the fact that autumn-fixed specimens of *H. ordunensis* clearly show the band while it is not so conspicuous in spring-fixed specimens, suggests that the expression of the band is influenced or masked by physiological causes and that the appearance of the band may be modified by the hypotonic treatment, the fixation and staining methods employed.

These reasons lead us to expect that the clear band occurs in other species, some of which already have been studied, although the band was not reported in them. The band might be seen if the snails are studied during the appropriate season.

ACKNOWLEDGEMENTS

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THE REPRODUCTIVE STRATEGY OF THE MANGROVE BIVALVE *POLYMESODA (GELOINA) EROSA* (BIVALVIA: CORBICULOIDEA) IN HONG KONG

Brian Morton

ABSTRACT

Monthly samples of the tropical Southeast Asian bivalve *Polymesoda (Geloina) erosa* were collected from a mangrove in Hong Kong over the course of one year. Each individual clam, following shell measurement, was sectioned and sexed, the condition of the gonad (primordial, immature, maturing, mature, spent) being referred to a scale of 1-5 for both sexes. *P. erosa* is dioecious, the samples comprising 51.5% females, 38.5% males, 0.5% simultaneous hermaphrodites, and 9.5% of the individuals of indeterminate sex. Individuals mature at a shell length of about 35 mm and reproduction occurs over a single, extended phase, during summer. Fertilised eggs are not brooded in the ctenidia as in other corbiculids. The expression of sexuality in *P. erosa* is similar to that of other marine veneroids, but it also can be seen as the simpler archetype of the more reproductively specialized freshwater members of the Corbiculoidea.

INTRODUCTION

It is generally assumed that the freshwater representatives of the Corbiculoidea are derived from a marine ancestor (Keen & Casey, 1969). Certainly the Veneroida are widely dominant in inshore marine assemblages. The Veneroida generally have a relatively simple reproductive strategy in which dioecious individuals release large numbers of oligolecithal eggs for fertilisation in the sea. According to Coe (1943), about 96% of all bivalves are gonochoristic (dioecious). A good example in the Veneroida is *Anomalocardia squamosa* Lamarck (Morton, 1979).

The freshwater Corbiculoidea, e.g., *Corbicula fluminea* (Müller) and *C. fluminalis* (Müller) (Morton, 1977a; 1982a), on the other hand, have more complicated, but different reproductive strategies. The former is dioecious or hermaphroditic, incubating fertilised eggs in the inner demibranch, and releasing pediveligers. Recently, Morton (1983a) has shown that in lentic and lotic waters strategies in this species differ. *C. fluminalis* is dioecious, with a trend towards protogyny, but with a percentage of the population simultaneous hermaphrodites. It is possible that, among the more brackish-water representatives of the Corbiculoidea, simpler reproductive strategies prevail as representative of intermediate conditions between the respectively simpler and more complex reproductive cycles of the marine and freshwater Veneroida. This study investigates the reproductive strategy of the Southeast Asian mangrove corbiculid bivalve *Polymesoda (Geloina) erosa* (Solander).

In Hong Kong (and the rest of Southeast Asia), the mangal is colonised by a number of highly specialised bivalves (Morton, 1983b). *Polymesoda erosa* is high-zoned, half buried in the mud around streams draining through the forest. It possesses a number of adaptations, largely physiological, to this high-zoned life, where it may be emersed for long periods of time.

MATERIALS AND METHODS

In Hong Kong, *Polymesoda erosa* is, as with the mangroves themselves, approaching the northern limit of its range. Accordingly, from Hong Kong's limited mangrove stands, it has not been possible to obtain large samples of *Polymesoda* (as has been possible for the freshwater corbiculids earlier studied). However,

from a small mangrove at Shuen Wan in Tolo Harbour, New Territories, Hong Kong, between 8-16 specimens of *Polymesoda* were collected every month for 13 months commencing in February 1980. A total of 169 individuals were collected. Each specimen was measured along its greatest length, fixed in Bouin's fluid and then sectioned transversely through the middle of the visceral mass (with ctenidia attached). Alternate slides were stained in Ehrlich's haematoxylin or Masson's trichrome. The gonads of the sectioned specimens were sexed. The condition of the gonads was estimated by reference to five condition indices, namely, 1 = primordial; 2 = immature; 3 = maturing; 4 = mature; 5 = spent. These indices were based approximately upon those defined by Loosanoff (1937; 1942), Shaw (1964; 1965) and Morton (1982a,b).

RESULTS

Polymesoda (Geloina) erosa is dioecious; of the 169 specimens sectioned, there were 87 females, 65 males (with an additional 16 of undetermined sex) and only one hermaphrodite. Using the indices of gonad maturity established above, the pattern of reproduction can be established (Table 1; Plate 1). There is only one phase of reproduction in a year. Between March and May, the gonads of virtually all specimens were in an immature state, but they contained identifiable sex cells and therefore they could be defined as primordial males (Pl. 1, A_1) or females (Pl. 1, B_1). In the latter, small developing oocytes line the germinal epithelium, while in the former there is a germinal epithelium producing round, lightly staining primary spermatocytes. However, many individuals were so immature that it was impossible to determine their sex.

Active gametogenesis commenced in the Spring months of April and May, so that in June mature gametes were found. The developing gonads (condition 2) (Pl. 1, A_2; B_2) comprised enlarging seminiferous tubules and ovarian follicles with relatively narrow lumina. In males (Pl. 1, A_2), primary and secondary spermatocytes were present with some spermatids. In females (Pl. 1, B_2), prominent oogonia bulged from the follicle wall and in some they were attached to the wall by a broad-based stalk. Oogonia at this time were some 10 μm in diameter, with lightly staining yolk and an indistinct nucleus.

During May, June and July, the gonads generally were maturing. Maturing oogonia are very characteristic (Pl. 1, B_3), often still being attached to the follicle wall, but having a

TABLE 1. The sexual stages of individual clams in the monthly samples.

Month	Sex			
	Males	Females	Undetermined	Hermaphrodite
February	4,5,1,5,5,2*	5,5,4,1,5	1	
March	1,5	2,2,5,1,2,1,2,1,1,1	1,1	
April	4,3,1,2	3,1	1,1	
May	2,2,1	4,2,2,3	1,1,1,1,1,1	3
June	3,4,4,3	2,3,4,4,4,4,4,3,4	1,1	
July	3,4,4,3,4,3	4,1,3,4,4	1,1	
August	4,4,4,4,4,4	4,4,4,4,4,3,3,5,5	1	
September	5,5,5,5,4,4,5,4,5	5,4,5,5,5		
October	5,5,5,5	5,5,5,4,5,4,5,5,5		
November	4,5,5,5,4,5	5,5,5,4,4,5,5		
December	5,4,5,5,4,5,5,5,5	5,5,4,5,4		
January	5,5,5,5	5,5,5,4,5,5,5		
February	5,1,1,5,4,5	5,5,1,5,4,5		

*1 = primordial; 2 = immature; 3 = maturing; 4 = mature; 5 = spent.

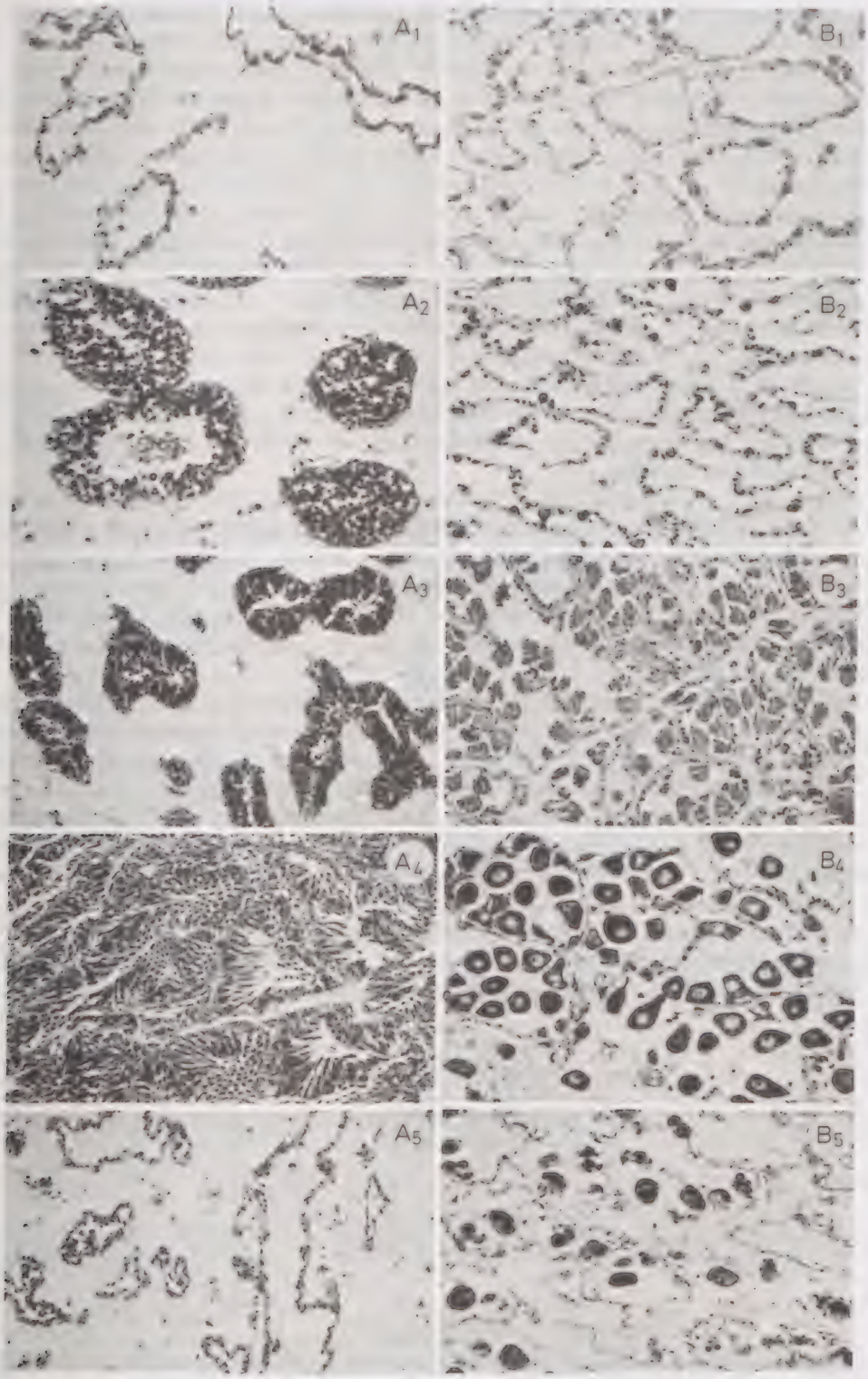

PLATE 1. Sexual phases of spermatogenesis (A_1-A_5) and oogenesis (B_1-B_5). The subscripts refer to the following conditions: 1 = primordial; 2 = developing; 3 = maturing; 4 = mature; 5 = spent. (Not all photographs are to the same scale.)

"stellate" appearance, the egg wall being crinkled by radiating pseudopodial processes. It seems possible that at this time the oogonia were actively absorbing soluble nutrients. By this stage they have attained a diameter of 40 μm and the nucleus was still indistinct, but with a well-defined nucleolus. Eggs free in the centre of the lumen were larger and more rounded. The seminiferous tubules (Pl. 1, A_3) were much larger and round spermatids were most abundant, some 2.5 μm in diameter, with a few spermatozoa having a long thin nuclear head 6 μm long.

Mature gonads (Pl. 1, A_4; B_4) first became numerous in June and thereafter occurred in July and August with, during this time, an approximately equal number maturing and a few spent. The mature eggs were some 60 μm in diameter and each had a large, vesicular nucleus 30 μm in diameter and a prominent nucleolus. Mature eggs were spherical and unattached to the follicle wall. They never packed the follicles, so it may be that upon maturity they are progressively released over a long period. The seminiferous tubules at this time are very characteristic, the tubule wall being thrown into long (160 μm) cords that project into the tubule lumen. Attached to these, head inwards, are the spermatozoa. Clusters of these spermatozoa may be pinched off apically from the cords to form spherical morulae (as in *Corbicula fluminalis* (Morton, 1982a)), some 20 μm in diameter, but in the fully mature tubules the sperm seem to fill the lumen as a mass.

From September until the following February, the majority of the gonads were spent (Pl. 1, A_5; B_5), the follicles progressively occurring with fewer and fewer mature eggs, the shed ones not being replaced by new oogonia. The lumina come to be filled with necrotic material that eventually is lost, and the follicles reassume their flaccid, empty appearance typical of the primordial condition. A similar situation occurs in the seminiferous tubules. As the spermatozoa are shed, they are not replenished and the tubules shrink, necrotic material accumulating in the lumina.

By sexing the specimens constituting the individual monthly and accumulated monthly samples, it can be seen (Fig. 1) that there is no distinction with regard to size and numbers between males and females throughout the size range of the species. Immature individuals generally are less than 35 mm in length. Thus, juveniles mature into either males or females.

From Fig. 2, it can be seen that the highest incidence of immature individuals occurs from March to May, and that in each monthly sample there is again an approximately equal division of males and females. Thus, both in terms of space and time, there is no question of consecutive hermaphroditism (although one specimen of the 169 was a simultaneous hermaphrodite); *Polymesoda erosa* is dioecious, with a long, single, summer breeding season.

The ctenidia of the sectioned specimens also were examined for glands typical of corbiculids which brood their eggs, e.g., as in *Corbicula fluminea* (Morton, 1977b,c). None were found.

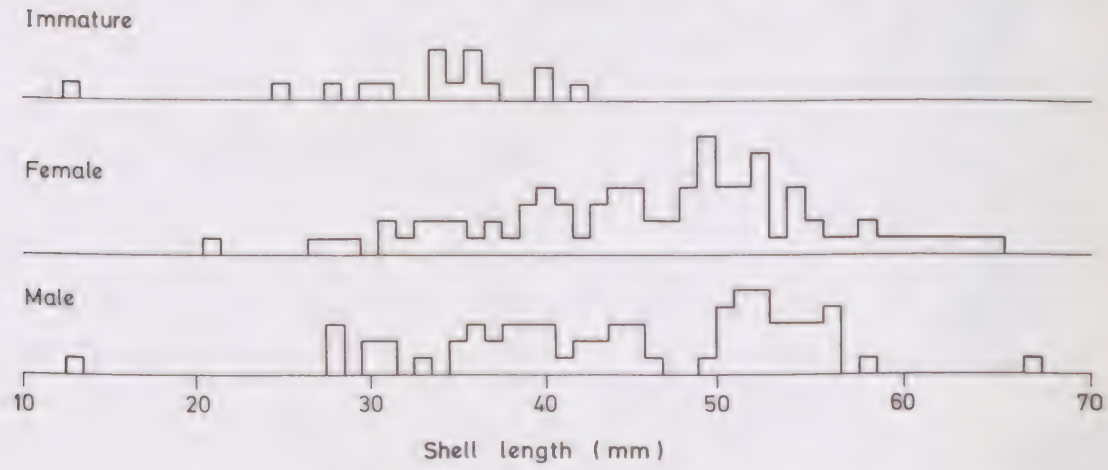

FIG. 1. The incidence in the accumulated samples of immature male and female individuals.

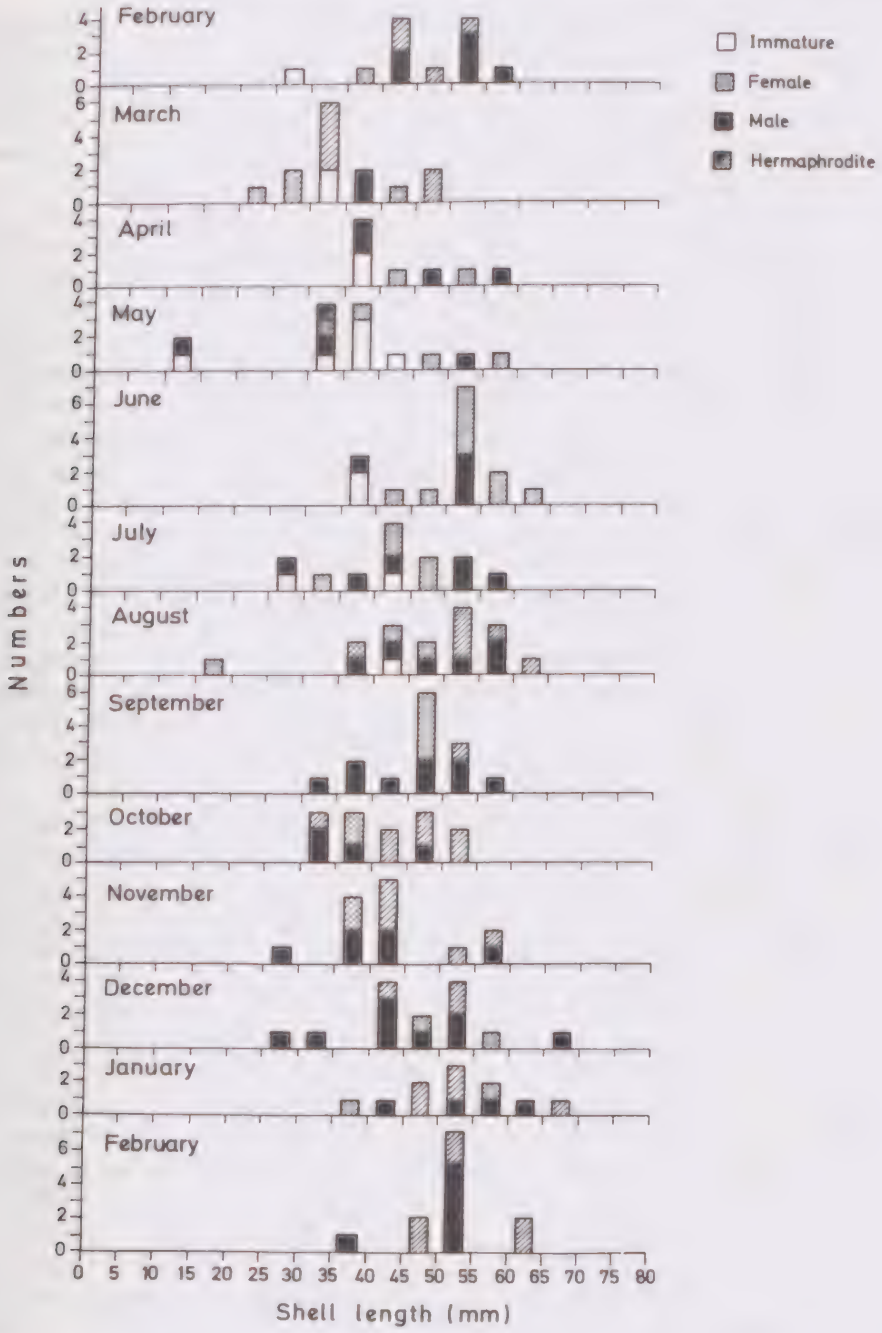

FIG. 2. The incidence of immature individuals, males and females in the monthly samples from February 1980 to February 1981.

DISCUSSION

Polymesoda (Geloina) erosa from the Hong Kong mangrove is dioecious and has no unusual sexual adaptations, i.e., unlike the closely related *Corbicula fluminea* in fresh waters, *P. erosa* does not retain fertilized eggs within the supra-branchial chamber (Morton, 1977a). Within the population as a whole, there was a majority of females (87; 51.5%) against males

(65; 38.5%) (as is typical of fresh- and brackish-water bivalves, e.g., *C. fluminalis* and *Limnoperna fortunei* (Dunker) (Morton, 1982a,b)). Sixteen (9.5%) individuals were of undetermined sex, and one (0.5%) was a hermaphrodite. A small percentage of hermaphrodites seems to be characteristic of some otherwise dioecious species, e.g., *Dreissena polymorpha* (Pallas) (Antheunisse, 1963) and *C. fluminalis* (Morton, 1982a). The females produce, over a long period of time, oligolecithal eggs about 60 μm in diameter, and the males produce large numbers of sperm.

The gonads commence maturing in Spring (March to May) and by early summer they are mature. Mature gonads have been shown to occur in the population from June through to Autumn, i.e., broadly coinciding with high summer temperatures, so that the period of potential breeding is exceptionally long, implying that there are not distinct periods of gamete release. Typically, other freshwater bivalves in Hong Kong (i.e., *Corbicula fluminea* and *Limnoperna fortunei*) (Morton, 1977a; 1982b) have two breeding seasons in any one year, i.e., one breeding season in early summer and one in late summer. In the intertidal bivalve *Anomalocardia squamosa*, there is a similar long breeding season (Morton, 1979), which may be divided into two phases which are masked by an almost continuous pattern of larval settlement, because of the large numbers of progeny released. However, a single, long, summer breeding cycle would fit in well with the distribution of *Polymesoda erosa* in tropical Indo-Pacific mangroves. Similarly, *C. fluminalis* has a single reproductive phase, but it occurs in winter because in southern China the species is approaching the southern limit of its range (Morton, 1982a).

The shells of *Polymesoda erosa* always are badly eroded by the acid mangal soils, making age determination by counting growth rings impossible. The older rings are always destroyed first. Individuals of *P. erosa* mature at an approximate length of 35 mm (Fig. 1), and it also can be seen (Figs. 1, 2) that the May and August samples included small shells which may represent the result of the previous year's spawning.

The simple reproductive strategy of *Polymesoda erosa* is surprising, because this clam occupies an extremely difficult niche in the mangrove system. This high-zoned species (and *P. proxima*) has other remarkable adaptations enabling it to survive extended periods of emersion. These include the ability to collect subterranean water and detrital food through the pedal gape (Morton, 1976); feeding in response to immersion, either by rain or the tide (Morton, 1975); and being able to survive (up to three months) long periods of desiccation (Morton, unpubl. data). The simple reproductive strategy is, however, of especial interest with regard to the postulated course of evolution of the Corbiculoidea. It has been suggested that the Corbiculoidea arose from a veneroid, marine ancestor (Keen & Casey, 1969). The simple reproductive strategies of many intertidal members of the Veneroida (e.g., *Anomalocardia squamosa* (Morton, 1979)) and *P. erosa* would support this. The simple reproductive strategy of *P. erosa* has, however, implications for the more specialised freshwater members of the Corbiculoidea. Thus, the Asian riverine *Corbicula fluminalis* also is dioecious, but has a trend towards protogyny. There also are a few true, simultaneous hermaphrodites within the population. *C. fluminalis* also has one breeding season per year and the trend towards protogyny may be considered to be a specialisation allowing occupation of a range of lentic environments.

The essentially stream-dwelling *Corbicula fluminea*, however, has a variable reproductive strategy (Morton, 1983a) and incubates its fertilized eggs and larvae until they reach the crawling pediveliger stage. These adaptations suit it to ecologically unstable tropical lotic waters. *C. fluminalis* develops glands within the inner demibranch of the gill, but does not incubate its eggs. The same glands in *C. fluminea* provide nourishment for the developing larvae. *Polymesoda erosa* thus can be seen as the reproductively simpler archetype of the more specialised Corbiculoidea, in which the colonisation of fresh waters has been achieved by reproductive specialisations (with associated enhanced powers of osmoregulation) (Gainey & Greenberg, 1977). The development of ctenidial glands in *C. fluminalis* must be seen as an evolutionary pre-adaptation, perhaps fulfilling an as yet unknown function in this bivalve, which has subsequently permitted larval brooding in *C. fluminea*.

In *Polymesoda erosa*, behavioural and physiological adaptations suit it to a life in the tropical mangal. In the lentic and lotic Corbiculoidea, adaptations are limited essentially to the reproductive system.

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THE SALINITY TOLERANCE OF *CORBICULA FLUMINEA* (BIVALVIA: CORBICULOIDEA) FROM HONG KONG

Brian Morton and K.Y. Tong

ABSTRACT

The salinity tolerance of the Asian freshwater corbiculid clam, *Corbicula fluminea*, has been tested by assessing mortality, tissue chloride and body water content in salinities ranging from 0.0-34.5°/oo. At salinities below approximately 13.0°/oo, *C. fluminea* can osmoregulate, maintaining fairly constant tissue chloride levels for periods of up to seven days, with little mortality. At higher salinities, *C. fluminea* osmoconforms and mortality progressively increases with salinity and time.

These data correlate well with those obtained for *C. fluminea* elsewhere, notably the U.S.A., where this species has been introduced. A less conclusive correlation is made with data obtained for *C. leana* from Japan.

INTRODUCTION

The fresh waters of Asia are widely colonised by *Corbicula fluminea* (Müller 1774) or by other "species", forms or races, all of which can be related to the highly variable *C. fluminea* (Morton, 1979; 1984). *C. fluminea* also occurs in the U.S.A., where it has been introduced. Early literature reports refer to this as *C. manilensis* Philippi (Clench & Stansbery, 1969), but this is also a junior synonym of *C. fluminea* (Morton, 1979). For southern China, Morton (1984) has proposed a two-species model: *C. fluminea* inhabiting fresh water and *C. fluminalis* (Müller 1774) in brackish water. A similar model seems to hold true for much of Asia and Africa, but in Japan the fresh- and brackish-water species are *C. leana* Prime and *C. japonica* Prime; Morton (1984), however, considered these two nominal species to be but junior synonyms of *C. fluminea* and *C. fluminalis*, respectively.

Fuji (1957a) has reported on the salinity tolerance of *Corbicula japonica*, but, because of growth rate data that more closely approximate *C. fluminea* (Fuji, 1957b), the species he was researching might have been *C. leana* (= *C. fluminea*) (Morton, 1984). Accordingly, the salinity tolerance study of *C. japonica* and *C. leana* by Kado & Murata (1974) is used here primarily for comparative purposes. Similarly, in the U.S.A., Gainey & Greenberg (1977) have studied the salinity tolerance of *C. manilensis* (= *C. fluminea*). The former authors reported that *C. leana* can osmoregulate to a salinity up to approximately 5°/oo; the latter authors concluded that *C. fluminea* is an osmoregulator in salinities of up to 3°/oo, but they set an upper tolerance limit of 14°/oo for this species.

This study reports upon the salinity tolerance of *C. fluminea* in Hong Kong.

MATERIALS AND METHODS

Specimens of *Corbicula fluminea* were obtained from the flooded furrows of vegetable gardens at Ping Long in the Lam Chuen River valley of the Hong Kong New Territories. On return to this laboratory, the bivalves were held for one week in a stock tank of aerated (fresh) pond water and fed with finely ground fish food (Tetramin). Ten litres of the following sea water dilutions were made: 0.0°/oo, 1.0°/oo, 2.0°/oo, 3.0°/oo, 4.0°/oo, 5.0°/oo, 7.0°/oo, 10.0°/oo, 13.0°/oo, 17.0°/oo, 21.0°/oo, 27.0°/oo and 34.5°/oo (sea water). Into each tank was placed 100 specimens of *C. fluminea*, ranging in length from 10.5-20.5 mm. The tanks were filtered, aerated, maintained at ambient temperature (approximately 20.0°C ± 2.0°C) and the bivalves fed with Tetramin. Mortality was recorded daily and cumulative % mortality calculated. Dead specimens (those with gaping shells and not responding to mantle stimulation) were removed immediately.

From separate stocks within the tanks, three specimens, ranging in shell length from 13.0-15.5 mm, were removed at intervals of one, two, three, five and seven days post-initiation. The tissues of each were

removed, blotted dry and fresh weight recorded. They were then dried at 70°C to constant weight and subsequently ground and mixed with distilled water. Each sample was then centrifuged at 3,000 rpm for 20 min and the supernatant collected and diluted to 25 ml. Determination of chloride was done by titration with 0.01 M silver nitrate using 1 ml of potassium chromate indicator. Calculated tissue chloride values were obtained and expressed as mg chloride g^{-1} dry tissue. The body water content of an individual equalled the difference between fresh and dry weights and was expressed in terms of percentage fresh weight. The mean of the three individuals comprising each sample was taken after days one, two, three, five or seven in the different test salinities.

Voucher specimens of *Corbicula fluminea* used in this study have been deposited in the United States National Museum of Natural History, Washington, D.C., U.S.A. [cat. no. 841303].

RESULTS

Consider first cumulative mortality (Fig. 1). At salinities less than 10°/oo, 1% mortality was recorded after seven days. At 13°/oo, 5% mortality occurred after six days. At salinities between 17.0°/oo and 34.5°/oo, however, mortality rates dramatically increased from days two to three onwards such that, within seven days, virtually all of the *Corbicula* specimens maintained in these salinities had died. It possibly is significant that little mortality of these individuals occurred on the first and second days of the experiments.

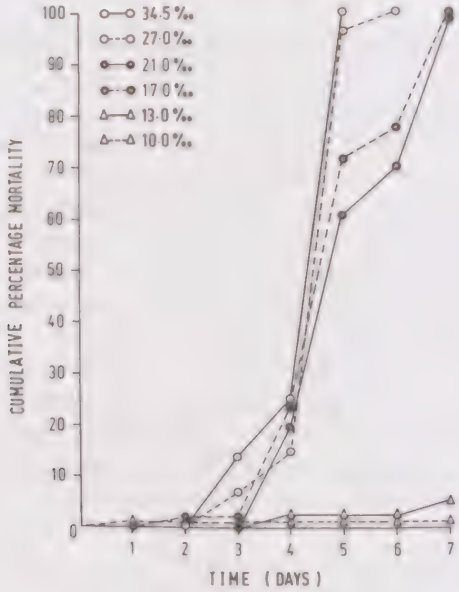

FIG. 1. *Corbicula fluminea*. The cumulative percentage mortality at different salinities.

With regard to tissue chloride, Fig. 2 shows that, at salinities between 0-10°/oo, levels fluctuated but little between 18-28 mg Cl g^{-1} dry tissue. At a salinity of 13°/oo, tissue chloride levels increased rather sharply to in excess of 40 mg Cl g^{-1} after day three and 50 mg Cl g^{-1} at day seven. At salinities between 17.0°/oo and 34.5°/oo, sharp rises in tissue chloride levels to between 30-46 mg Cl g^{-1} were recorded after day two, between 45-60 mg Cl g^{-1} after day three, 45-70 mg Cl g^{-1} after day five and 58-100 mg Cl g^{-1} after day seven. Records for animals in a salinity of 34.5°/oo after day five were not available, all having died.

Fig. 3 illustrates tissue chloride levels in relation to the external chloride concentrations after three days. At salinities between 0-10°/oo, tissue chloride levels remained fairly constant between 16-25 mg Cl g^{-1}. Between salinities of 17-27°/oo, tissue chloride levels remained relatively constant at around 45 mg Cl g^{-1} but thereafter rose sharply to 62 mg Cl g^{-1} at 34.5°/oo.

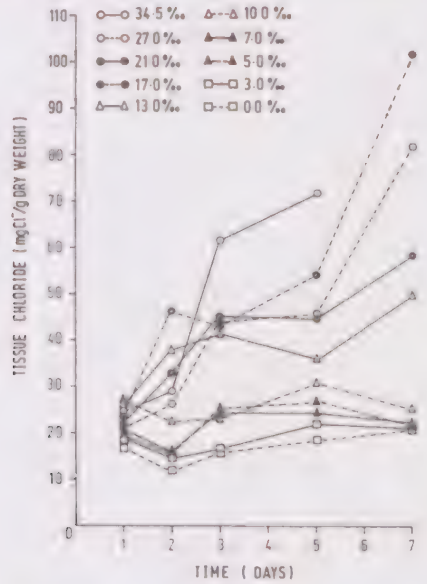

FIG. 2. *Corbicula fluminea*. The tissue chloride content of individuals held in different salinities in relation to time. Each point represents the mean of three individuals.

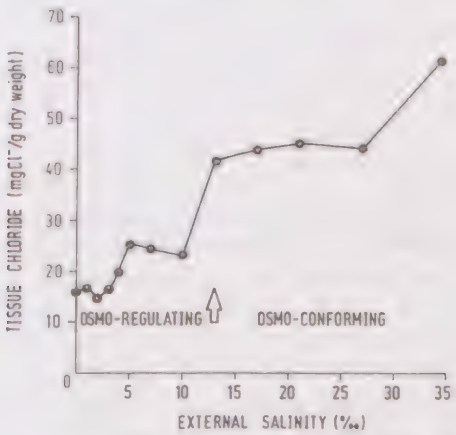

FIG. 3. *Corbicula fluminea*. The tissue chloride content of individuals held for three days in waters of different salinities. Each point represents the mean of three individuals.

The % body fluids fluctuated little over the course of the experiment (Fig. 4) and ranged between 78.5% and 86.2%. For virtually all salinities, however, a pronounced decline in body water weight occurred between days one and two, and thereafter progressively returned to normal.

DISCUSSION

Gainey & Greenberg (1977) have shown that *Corbicula manilensis* (= *C. fluminea*) is an osmoregulator in salinities less than 3.0°/oo but becomes an osmoconformer at salinities greater than this. They set an upper tolerance limit of 14°/oo for this species. Evans et al.

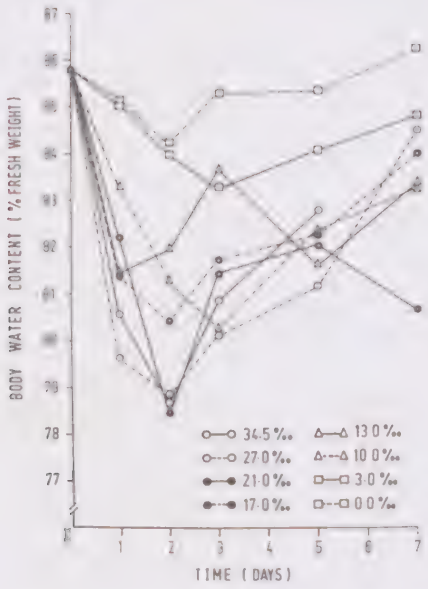

FIG. 4. *Corbicula fluminea*. The body water content (% of fresh weight) of individuals held in different salinities in relation to time. Each point represents the mean of three individuals.

(1979) reported that the critical tolerance limit for all their shock-exposed test populations of *C. fluminea* was between 10-12°/oo. Kado & Murata (1974) reported an upper tolerance limit of 70% sea water (≃24°/oo) for *C. japonica* (= *C. fluminalis*) and 15% sea water (≃5.0°/oo) for *C. leana* (= *C. fluminea*).

From the data presented here for *Corbicula fluminea*, it seems clear that this freshwater species can osmoregulate, for short periods of at least seven days, in salinities up to 13°/oo. Between this salinity and 17.5°/oo, *C. fluminea* becomes an osmoconformer and the resulting hypertonicity of the body fluids results in progressively increased mortality. At salinities below 10°/oo, *C. fluminea* can maintain a body tissue chloride level of around 30 mg Cl g^{-1}. At a salinity of 13°/oo, mortality does not increase significantly even when tissue chloride levels attain 35 mg Cl g^{-1}. At salinities above this, however, tissue chloride levels rise dramatically. For all test animals, the rise in tissue water content, following an initial two to three day decline, can be seen as additional evidence of an attempt to osmoregulate. However, at salinities greater than 13°/oo, chloride regulation appears impossible and death ensues.

These data provide physiological evidence to support the claim (Britton & Morton, 1979; Morton, 1979, 1984) that *Corbicula fluminea* has been introduced into the U.S.A. Thus, Gainey & Greenberg (1977) recorded an osmoregulation figure for this species in the U.S.A. of 14°/oo; we recorded a figure probably slightly in excess of 13°/oo (our test salinities being 13°/oo and 17°/oo) for *C. fluminea* in Hong Kong. It is difficult to correlate this work with that done on *C. japonica* and *C. leana* in Japan by Kado & Murata (1974), because their data are expressed in terms of % sea water and not actual salinities. However, *C. fluminea* cannot regulate to the (estimated) salinity of 24°/oo recorded for *C. japonica* (an inhabitant of "muddy sand bottoms in brackish waters of shallow estuarines [sic] or lakes") (Kado & Murata, 1974). The fewer tests undertaken upon *C. leana* (i.e., 5%, 10%, 25%, 50%, 75% and 100%) by Kado & Murata may not have allowed the finer discrimination of the critical regulation values of 14°/oo and 13°/oo obtained by Gainey & Greenberg (1977) and in this study. Morton (1984) has suggested that *C. japonica* and *C. leana* are the "local" names respectively applied to *C. fluminalis* and *C. fluminea* in Japan. It has not yet been possible

to determine the upper (and perhaps just as important, the lower) salinity tolerance limit of *C. fluminalis* (the species does not occur within the territorial waters of Hong Kong). This is an aim, however, to permit comparison with *C. japonica*.

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CONVERGENCE IN BIVALVE CONCHIOLIN LAYER MICROSTRUCTURE

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ABSTRACT

Conchiolin layers occur within the shells of representatives of three brackish-water and marine bivalve superfamilies and are ubiquitous among freshwater Unionacea. Conchiolin layers examined exhibit a high degree of convergence in microstructure, despite their occurrence in distantly related taxa. These convergences are hypothesized to have arisen through similarity of response to similar selection pressures and constraints on the number of ways such conchiolin layers can be constructed. Conchiolin layers are hypothesized to broaden environmental tolerances of bivalves possessing them, since it allows such bivalves to inhabit waters of low calcium availability and affords some resistance to chemically boring predators.

INTRODUCTION

The way bivalves and gastropods construct their shells is of fundamental importance to their ability to resist desiccation and various types of predation, as well as the ease by which they move on and through the substratum (Stanley, 1969, 1981; Linsley, 1978; Vermeij, 1978; Palmer, 1979; Kat, 1981; Signor, 1983). Similarly, shell microstructural components can be important in increasing the durability and hardness of mollusk shells. For example, freshwater bivalves of the families Unionidae, Mutelidae and Margaritiferidae possess conchiolin layers within their shells which allow these bivalves to resist dissolution in acidic or poorly buffered fresh waters once the periostracum has worn away (Tolstikova, 1974; Tevesz & Carter, 1980; Kat, 1982, 1983a). Freshwater bivalves of the family Corbiculidae that lack such internal layers can suffer heavy mortality due to shell dissolution in habitats where co-occuring unionids suffer comparatively little damage (Kat, 1982).

Despite the occurrence of shell dissolution among marine taxa, the extent to which similar conchiolin layers occur in the shells of marine bivalves has not been adequately investigated. One notable exception is a study of the Corbulidae by Lewy & Samtleben (1979). Corbulids in general are slow and shallow burrowers, and inhabit marginal marine environments characterized by low salinity, oxygen content, and calcium carbonate availability. Lewy & Samtleben (1979) postulated that conchiolin layers among corbulids prevent shell dissolution in such habitats, and that these layers also can act as barriers to prevent chemically boring organisms from penetrating the shell. Many boreholes certainly terminate at the conchiolin layers of these bivalves (see Lewy & Samtleben, 1979, fig. 2E, F). Interestingly, the corbulid conchiolin layers apparently resemble those among the Unionidae in a number of structural features (Kat, 1982).

This study was undertaken to determine the extent to which conchiolin layers occur among brackish-water and marine bivalves, and the extent to which convergence in microstructural details occurs among distantly related taxa. Representatives of nine marine and brackish-water bivalve families (Arcticidae, Corbiculidae, Corbulidae, Hyatellidae, Mactridae, Psammobiidae, Solenidae, Solenocurtidae and Tellinidae) were examined and compared with bivalves of two freshwater families (Margaritiferidae and Unionidae). Species were chosen on the basis of occurrence in estuarine habitats and/or marine habitats with soft, organic-rich sediments. Such species often exhibit considerable shell wear in the umbonal region of the

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valves and consequently can be expected to experience selection to reduce shell dissolution. The bivalve species examined are listed in Table 1.

MATERIALS AND METHODS

Specimens for this study were obtained from malacological collections at the Academy of Natural Sciences of Philadelphia and the National Museums of Kenya (Table 1). Use of such specimens involves a drawback, in that environmental information is often missing or presented in an extremely generalized fashion. Differences in environmental conditions experienced by various populations of a species could, for example, affect the relative sizes of various components of the conchiolin layers. However, experience with freshwater bivalves (see Kat, 1983a,b) indicates that, while environmental conditions can influence the number of layers deposited within the shell, microstructure of these layers is not affected by environmental differences among populations. All specimens examined were adults.

TABLE 1. Classification, habitat type, collection locality and catalogue numbers (KNML = National Museums of Kenya, Division of Mollusks; ANSP = Academy of Natural Sciences of Philadelphia) of the species examined. Species marked with an asterisk possess conchiolin layers.

Unionoida			
Unionidae			
Elliptio complanata (Lightfoot)*	Freshwater	Maryland, U.S.A.	KNML 1134
Caelatura leopoldvillensis (Putzeys)*	Freshwater	Zaire	KNML 1135
Lampsilis ochracea (Say)*	Freshwater	Nova Scotia, Canada	KNML 1136
Alasmidonta undulata (Say)*	Freshwater	Nova Scotia, Canada	KNML 1137
Margaritiferidae			
Margaritifera margaritifera (Linnaeus)*	Freshwater	Nova Scotia, Canada	KNML 1138
Veneroida			
Solenidae			
Glauconome rugosa (Reeve)*	Estuarine	Philippines	ANSP 52576
Pharella acutidens Broderip & Sowerby*	Estuarine	Philippines	ANSP 246162
Siliqua costata Say	Marine to brackish	Massachusetts, U.S.A.	KNML 1139
Corbiculidae			
Polymesoda caroliniana (Bosc)*	Estuarine	Georgia, U.S.A.	KNML 1140
Geloina suborbiculata (Pilsbry)*	Estuarine	Philippines	ANSP 224123
Mactridae			
Rangia cuneata Bosc	Estuarine	Virginia, U.S.A.	KNML 1141
Tellinidae			
Macoma balthica Linnaeus	Marine to brackish	Delaware, U.S.A.	KNML 1142
Solenocurtidae			
Tagelus plebeius Lightfoot	Marine to brackish	Delaware, U.S.A.	KNML 1143
Arcticidae			
Arctica islandica (Linnaeus)	Marine	Massachusetts, U.S.A.	KNML 1144
Psammobiidae			
Gari californica (Conrad)	Marine	California, U.S.A.	ANSP 34612
Myoida			
Corbulidae			
Varicorbula gibba (Olivi)*	Marine to brackish	England	KNML 1145
Corbula luteola Carpenter*	Marine to brackish	California, U.S.A.	ANSP 31262
Corbula smithiana Gould*	Marine to brackish	Australia	ANSP 33429
Hyatellidae			
Cyrtodaria siliqua (Spengler)	Marine	Florida, U.S.A.	ANSP 123641

Shells were embedded in clear plastic, radially sectioned with a circular rock saw, polished with a series of carborundum grit sizes, and etched for 5 sec in 5% HCl in preparation for scanning electron microscopy (SEM). During SEM, the specimens were tilted at an angle of about 25° to reveal clearly the microstructure of the reticulate portions of the conchiolin layers; the relative thickness of the outer homogeneous region of the layers is thus slightly distorted. Three specimens of each species, usually from different populations were examined to determine the amount of intraspecific variability in conchiolin layer microstructure.

RESULTS

Seven of the 14 marine and brackish-water bivalve species examined (see Table 1) possessed conchiolin layers. These seven taxa were distributed among two orders (Veneroida and Myoida) and three superfamilies (Solenacea, Corbiculacea and Myacea). In addition, conchiolin layers are ubiquitous among the Unionacea (Kat, 1983a). The study indicates a fundamental similarity in conchiolin layer microstructure among the taxa examined, but also that some differences exist. Dimensions of the conchiolin layers and their component parts are listed in Table 2. Details of the conchiolin layers of taxa examined can be summarized as follows.

Marine and brackish-water taxa

Varicorbula gibba (Olivi) (Fig. 1a)

The conchiolin layers of *Varicorbula gibba* were examined in detail by Lewy & Samtleben (1979), and this study confirms many of their observations. One and occasionally two (the Main Conchiolin Layer (MCL) and the Second Conchiolin Layer (SCL) of Lewy & Samtleben, 1979) conchiolin layers occur within the shell. The MCL extends from the umbonal region to the ventral margin of the left valve and to a groove between the pallial line and the ventral margin of the right valve. Corbulids in general are inequivalve, and the left valve fits into this groove in the right valve where the MCL emerges. The edge of the MCL was therefore compared to an elastic gasket by Lewy and Samtleben as it permits hermetic closure of the valves. The conchiolin layers are from 18-22 μm thick and are separable into two regions: an outermost homogeneous section and an innermost reticulate section composed of variously sized chambers of conchiolin that contain "cones" of calcium carbonate (see Lewy & Samtleben, 1979, fig. 5c-f; Fig. 1a of this study). The SCL lies under the MCL, is shorter than the MCL, and is similar in microstructure to the MCL, except that the homogeneous region of the SCL can be somewhat thinner.

Corbula luteola Carpenter (Fig. 1b)

The shell of *Corbula luteola* also contains two main conchiolin layers, but these layers differ in a number of aspects from those of *Varicorbula gibba*. First, seven to eight conchiolin layers are initiated in the umbonal region of the shell, but only two of these layers continue past the umbo to the ventral section of the valves. Second, the SCL in this species is apparently not deposited in a continuous sheet over the entire inner surface of the valve, as it pinches out near the middle of the valve and begins again near the ventral edge. And third, the microstructure of the conchiolin layers is different from that of *V. gibba*: the outer homogeneous section is thicker, and the inner reticulate region consists of dendritic structures oriented normal to the exterior of the valve. These dendritic structures are of different lengths and seem to end in organic sheets at the base of the layer. Calcium carbonate structures within the reticulate region could not be adequately observed since they largely dissolved during acid etching of the shells, perhaps indicating that these structures of *C. luteola* are more soluble than those of *V. gibba.*

Corbula smithiana Gould (Fig. 1c)

As was observed in the case of *Corbula luteola*, six to 10 conchiolin layers are initiated in the umbonal region of *C. smithiana*, of which at most two extend to the ventral edges of the

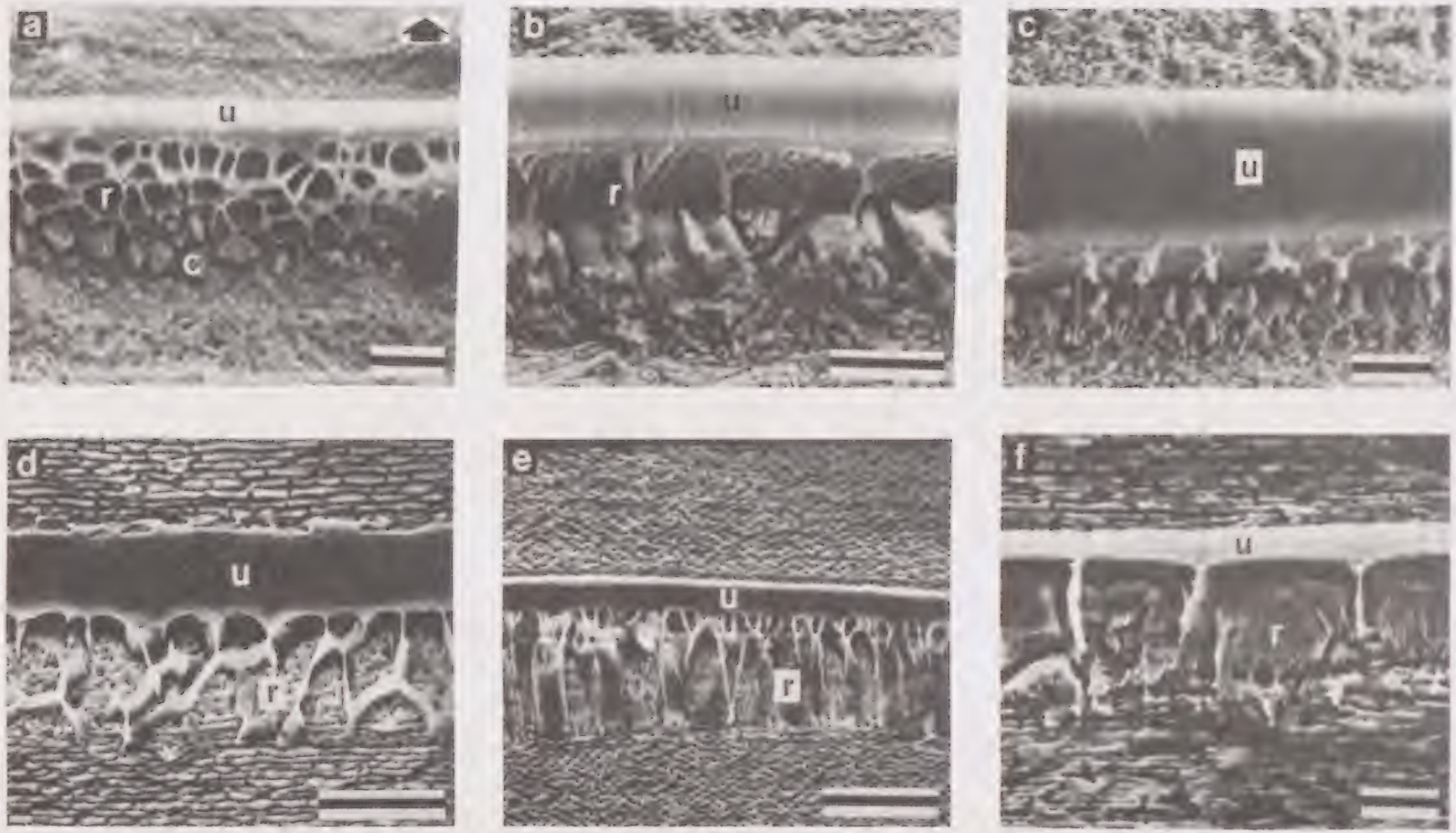

FIG. 1. Conchiolin layer of bivalve shells. a, *Varicorbula gibba*; scale bar = 10 μm. Arrow indicates direction to the outside of the shell. b, *Corbula luteola*; scale bar = 10 μm. c, *C. smithiana*; scale bar = 10 μm. d, *Elliptio complanata*; scale bar = 10 μm. e, *Margaritifera margaritifera*; scale bar = 20 μm. f, *Caelatura leopoldvillensis*; scale bar = 10 μm.

Abbreviations: c = calcareous structures within chambers of the inner reticulate region; r = inner reticulate region; u = outer homogeneous region.

TABLE 2. Dimensions of the conchiolin layers and their component sections.

Species	Conchiolin layer thickness (μm)		
	Total layer	Homogeneous section	Reticulate section
Varicorbula gibba	18-22	4-6	14-16
Corbula luteola	15-20	6-8	9-12
Corbula smithiana	16-22	14-18	2-4
Glauconome rugosa	4-8	4-8	–
Geloina suborbiculata	4-6	4-6	–
Polymesoda caroliniana	2-3	2-3	–
Pharella acutidens	2-3	2-3	–
*Elliptio complanata**	15-23	5-8	10-15
*Lampsilis ochracea**	4-6	4-6	–
*Alasmidonta undulata**	5-8	5-8	–
*Caelatura leopoldvillensis**	12-16	3-4	9-12
*Margaritifera margaritifera**	50-70	10-12	40-60

*Freshwater taxa.

valves. Shorter layers all terminate close to the umbo of the shell, and these short layers lie above, between and occasionally below the longer conchiolin layers. *C. smithiana* has the thickest (14-18 μm) outer homogeneous section observed among the conchiolin layers of the corbulids and other taxa examined here. The reticulate region, on the other hand, consists of little more than small projections into the underlying calcareous layers. Details of the lower surface of the outer homogeneous region, however, are similar to those of *C. luteola*. Calcareous structures in contact with the lower surface of the conchiolin layer seem to consist of vertical prisms or lamellae.

Polymesoda caroliniana (Bosc) (Fig. 2b)

Conchiolin layers within the shell of *Polymesoda caroliniana* are limited to the umbonal region of the valves and are among the thinnest observed in this study. The entire layer is only 2-3 μm thick and consists entirely of a homogeneous region with highly pitted or rugose upper and lower surfaces where the conchiolin layer contacts calcareous shell layers. No more than two conchiolin layers were observed within the shell of specimens examined.

Pharella acutidens Broderip & Sowerby (Fig. 2d)

Conchiolin layers of *Pharella acutidens* are similar in thickness to those of *Polymesoda caroliniana*, but they are much less rugose. The upper and lower surfaces of the conchiolin layers of this species are almost flat. In some sections of the conchiolin layer, however, small, fingerlike conchiolin projections extend downward into the underlying shell layers. The relationship of these projections to the surrounding calcareous layers could not be determined: the etching process removed sufficient calcium carbonate to cause these delicate structures to collapse onto each other. It is clear, however, that some of these structures are detached from the conchiolin layer itself and must have been formed between crystals of the shell layer.

Glauconome rugosa (Reeve) (Fig. 2c)

Numerous (6-10) conchiolin layers occur within the shell of *Glauconome rugosa*. Most of these layers are located in the umbonal region of the shell, while one to two layers continue

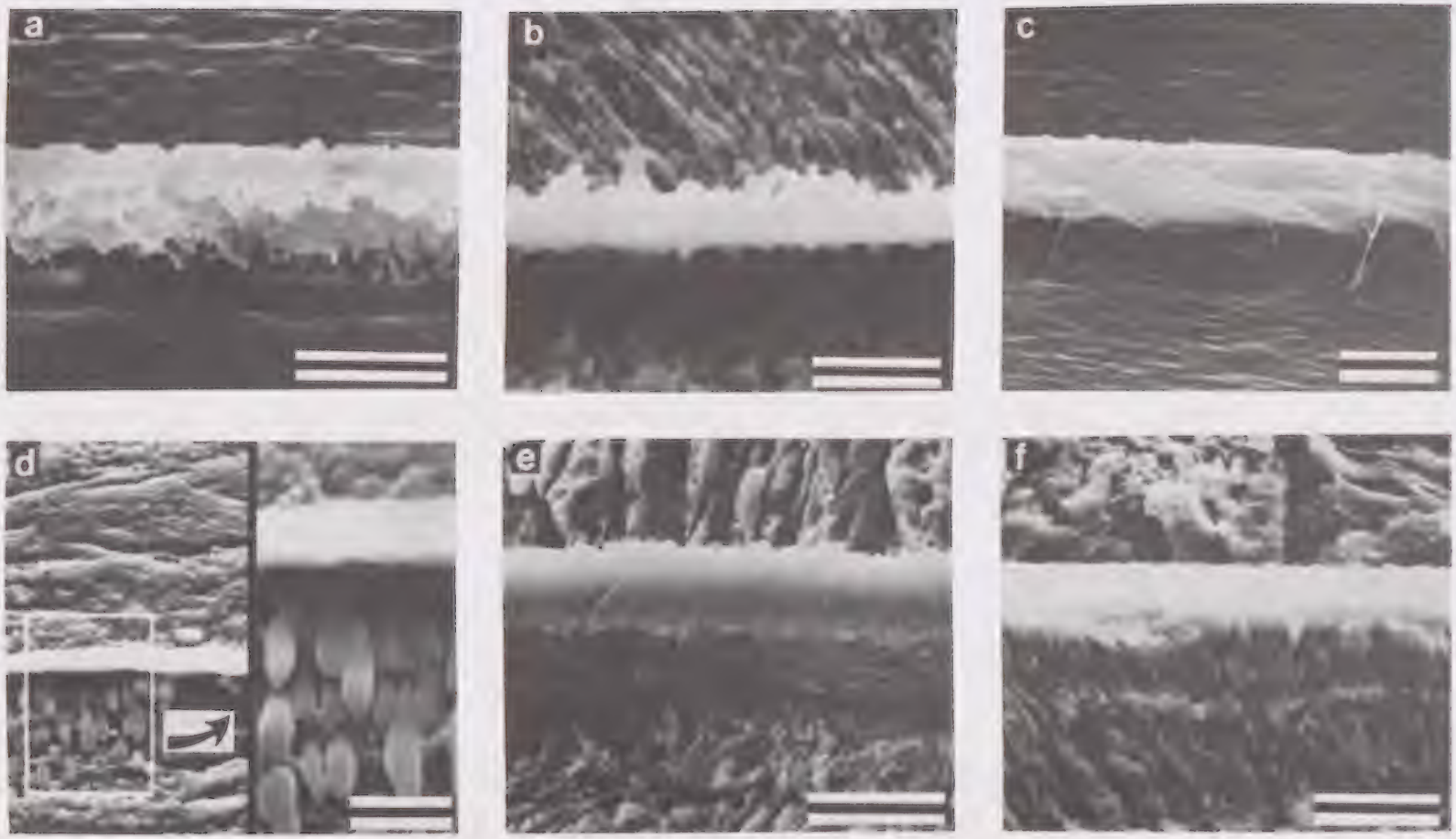

FIG. 2. Conchiolin layer of bivalve shells. a, *Alasmidonta undulata*; scale bar = 10 μm. b, *Polymesoda caroliniana*; scale bar = 5 μm. c, *Lampsilis ochracea*; scale bar = 10 μm. d, *Pharella acutidens*; region in box enlarged 2.5 at right. Scale bar = 10 μm on left, 4 μm on right. e, *Glauconome rugosa*; scale bar = 10 μm. f, *Geloina suborbiculata*; scale bar = 10 μm.

almost to the pallial line. The layers are simple in microstructure, consisting entirely of a homogeneous region of medium thickness (4-8 μm) with rugose surfaces.

Geloina suborbiculata (Pilsbry) (Fig. 2f)

Conchiolin layers of *Geloina suborbiculata* consist of homogeneous layers of medium thickness (4-6 μm), with a slightly developed reticulate region. No more than two such layers were observed to occur in the shell, and they are restricted to the region of the umbo.

Freshwater taxa: Margaritiferidae and Unionidae
(Fig. 1d,e,f; Fig. 2a,c)

Five species were selected from a more exhaustive survey of conchiolin layers among the Unionacea (see Kat, 1983a) to demonstrate the variety of conchiolin layer microstructures present among this freshwater group of bivalves. Conchiolin layers range from thick and complex (*Elliptio complanata* (Lightfoot), Fig. 1d; *Margaritifera margaritifera* (Linnaeus), Fig. 1e) through layers of intermediate complexity (*Caelatura leopoldvillensis* (Putzeys), Fig. 1f; *Alasmidonta undulata* (Say), Fig. 2a) to thin and comparatively featureless layers (*Lampsilis ochracea* (Say), Fig. 2c). Unionid species can possess conchiolin layers divisible into two types within the shell: thin and undifferentiated, and thick and more complex. Unionid complex layers can generally be divided into three regions: an outer homogeneous portion, a central, reticulate portion consisting of chambers of various shapes and sizes formed by sheet-like lamellae, and an inner, thin homogeneous layer (Kat, 1983a). Margaritiferids, on the other hand, possess only one type of layer, a thick complex band also composed of three regions: an outer, homogeneous portion, a central, vacuolated portion, and an inner, reticulate portion composed of widely spaced lamellae that form chambers filled with blocks of subprismatic shell material (Tolstikova, 1974; Kat, 1983a).

DISCUSSION

Given that the bivalve species possessing conchiolin layers belong to three separate orders, and that therefore these layers are likely of polyphyletic origin, the degree of convergence exhibited among the microstructure of these conchiolin layers is surprising. The similarities include the following.

1. Overall dimensions of the layers. For example, the conchiolin layers of *Geloina suborbiculata* (4-6 μm) and *Glauconome rugosa* (4-8 μm) are similar in dimension to those of freshwater taxa such as *Alasmidonta undulata* (5-8 μm) and *Lampsilis ochracea* (4-6 μm) examined here, and *Anodonta cataracta* Say (4-8 μm), *Strophitus undulatus* (Say) (3-5 μm) and *Lampsilis splendida* (Lea) (3-6 μm) examined earlier (Kat, 1983a). Also, the size of the reticulate region of the conchiolin layers of *Varicorbula gibba* (14-16 μm) and *Corbula luteola* (9-12 μm) compares closely with those of *Elliptio complanata* (10-15 μm) and *Caelatura leopoldvillensis* (9-12 μm). Nevertheless, marine taxa such as *Polymesoda caroliniana* and *Pharella acutidens* possess thinner conchiolin layers (2-3 μm) than have been observed among freshwater taxa (Kat, 1983a). Overall dimensions of the conchiolin layers and their component regions do not seem affected by environmental conditions among freshwater taxa, and have therefore been useful in taxonomic analyses (Kat, 1983a,b). More work needs to be done with marine taxa, however, to determine if constancy of dimensions of conchiolin layers among different environments is a general trend.

2. Location of the conchiolin layers. With the exception of the corbulids, conchiolin layers examined here are generally not deposited over the entire inner surface of the shell, but are localized in the umbonal region. Among unionids and margaritiferids, for example, conchiolin layers are deposited as patches of various sizes concentrated below the umbo.

This localization of conchiolin layers corresponds to the areas of the shell that are most often damaged by dissolution. The conchiolin layers of corbulids generally extend from the umbonal to the ventral region of the valves, and Lewy & Samtleben (1979) proposed that these layers not only retard shell dissolution but also seal the shell commissure and prevent shell penetration by boring organisms, which do not necessarily concentrate their activities in the umbonal region of the shell. Nevertheless, *Corbula luteola* and *C. smithiana* were both observed to possess numerous (6-10) conchiolin layers in the umbonal region, only two of which extended to the ventral parts of the shell. Why some conchiolin layers terminate in the umbonal region while others are secreted over more extensive parts of the inner surface of the shell is not known.

3. **Construction of conchiolin layers.** All conchiolin layers examined here consist of at least an outer, homogeneous region, and some taxa possess an additional inner, reticulate region. Both layers are in intimate contact with the surrounding shell layers, and conchiolin layers do not separate regions of different microstructure within the shell. Unionids that possess complex layers also can possess simple layers composed entirely of a homogeneous region: I have proposed elsewhere that unionid complex layers could result from elaborations on simple layers (Kat, 1983a). This is not true of marine and brackish-water taxa examined here nor of the margaritiferids, which possess only one type of layer in the shell. The complex conchiolin layers of corbulids examined in this study exhibit a remarkable number of similarities to those of the Unionacea. The most striking similarity is the division of complex layers into upper, homogeneous and lower, reticulate regions, and that the reticulate regions are generally composed of chambers or cells of conchiolin that enclose calcareous material of different microstructure from the rest of the shell (these differences are perhaps due to different crystallization environments). For example, the rounded chambers apparent in the conchiolin layer of *Varicorbula gibba* (Fig. 1a) are quite similar in appearance to those of *Elliptio complanata* (Fig. 1d) and *Margaritifera margaritifera* (Fig. 1e). Also, the chambers of the conchiolin layer of *Corbula luteola* (Fig. 1b) are similar in appearance to those of *Caelatura leopoldvillensis* (Fig. 1f) examined here and *Lampsilis radiata* (Gmelin), *Anodonta gibbosa* Say and *E. dariensis* (Lea) examined earlier (Kat, 1983a). However, the calcareous structures within the conchiolin reticulate region of *V. gibba* are of different microstructure than those of *E. complanata*, and the peculiar, fingerlike conchiolin structures associated with the conchiolin layer of *Pharella acutidens* have no parallel among freshwater taxa.

Why conchiolin layers exhibit convergences among these distantly related taxa could be due to similarities of response to similar selective pressures, constraints on the number of pathways by which the mantle can secrete a conchiolin layer, or both. For example, there seems to have been strong and ubiquitous selection for conchiolin layers firmly attached to the surrounding shell layers by pitted and rugose upper and lower surfaces. Such conchiolin layers could probably better withstand scour and the efforts of boring predators once the surmounting shell layers have been removed. It is not clear, however, why conchiolin layers composed of two or three different portions evolved in the lineages examined, and why they exhibit strong convergence in microstructure. The addition of a reticulate region to the homogeneous portion of a conchiolin layer certainly thickens the entire structure (although negligibly so in the case of *Corbula smithiana*), and inclusion of calcareous material within conchiolin layers could render the thickened layer more structurally sound. Incorporation of a chambered reticulate region might afford more flexibility than a completely homogeneous layer of equal thickness. Such flexibility could be important when underlying shell material has to be protected by conchiolin layers once the overlying shell has worn away. Conchiolin layers would then be performing a role analogous to that of the periostracum, and it is interesting to note that the periostracum and conchiolin layers are similar in microstructure among margaritiferids. Also, complex conchiolin layers among corbulids have been observed to deter chemically boring predators (Lewy & Samtleben, 1979), despite the ability of such predators to penetrate organic as well as mineral components of the shell (Carriker et al., 1978; Carriker,

1981). Since many corbulids exhibit boreholes that terminate at the conchiolin layers, it would be interesting to determine why boring predators terminate their activities at these layers, and whether it was a function of the complexity of the layer itself.

Despite the discussed advantages to incorporation of conchiolin layers in the shell, Lewy & Samtleben (1979) proposed that the presence of such layers within corbulid shells structurally weakens the valves which often split apart when the conchiolin layers are destroyed during fossilization. It is uncertain, however, whether shells possessing conchiolin layers are more susceptible to crushing by predators such as fishes and crabs (Vermeij, 1978; Palmer, 1979) than shells that do not have such layers, and therefore whether the incorporation of conchiolin layers compromises shell strength in living bivalves. The interdigitation of conchiolin layers with surrounding shell layers would seem to argue against a loss of shell structural integrity, but it is possible that very thick, almost entirely homogeneous conchiolin layers like those observed in *Corbula smithiana* could render the shell more easily breakable by crushing and shearing forces. This could explain the apparent paucity of such thick homogeneous layers among the taxa examined here and in Kat (1983a), and might be an additional advantage to thickening conchiolin layers by addition of a reticulate region rather than by addition of more homogeneous material.

The obvious success of freshwater members of the families Sphaeriidae, Dreissenidae and Corbiculidae, and the wide environmental tolerances of the other taxa examined here which lack conchiolin layers underline the fact that such layers are not a necessity for life in fresh, brackish and marine waters in which shell dissolution occurs. Even though bivalves without conchiolin layers often experience destruction of shell layers, high rates of compensatory shell secretion seem sufficient to prevent lethal shell dissolution in many of these species. Nevertheless, possession of conchiolin layers could allow a bivalve species to occupy a broader range of habitats both in terms of calcium availability and presence of chemically boring predators than bivalves that do not possess such layers.

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THE INTRODUCTION OF THE MEDITERRANEAN MUSSEL *MYTILUS GALLOPROVINCIALIS* INTO HONG KONG. – In recent years, a number of marine taxa have been introduced into Hong Kong. These include the bivalve *Mytilopsis sallei* Recluz (Morton, 1980; Huang & Morton, 1983), the slipper limpet *Crepidula onyx* Sowerby (Huang et al., 1983) and the isopod *Sphaeroma walkeri* Stebbing (Mak et al., 1984). Now we are reporting another introduction, *Mytilus galloprovincialis* Lamarck, a Mediterranean mussel that has been reported for areas outside the Mediterranean and its allied waters only recently: from the Atlantic coasts of Spain, Portugal, France and Britain (Seed, 1978), and from Japan (Hosomi, 1977; Wilkins et al., 1983). *M. galloprovincialis* has never been recorded south of 30° N latitude. Along the coast of mainland China, two species of *Mytilus* have hitherto been recorded: *M. edulis* Linnaeus and *M. coruscus* Gould (both thick-shelled with a ventral-ligamentary margin angle of ca. 30°) (Anonymous, 1982), both restricted to latitudes north of 25° N. No *Mytilus* has hitherto been recorded from the South China Sea. While *Mytilus* species characteristically are temperate, the environment of Hong Kong (lat. 22° N) is sub-tropical, with a mean monthly seawater temperature of 23°C and minimum and maximum means of 16° and 27.7°, respectively.

About 40 specimens of a purplish-black mussel not hitherto recorded locally have, since July 1983, been collected at low densities (<5 individuals per m^2) from a number of sites, covering areas from the estuarine west to the oceanic east, in the intertidal waters of Hong Kong (Fig. 1). Occurrence is most frequent in Victoria Harbour and, from the intertidal region of a concrete pier at North Point, 26 specimens ranging in length from 7.45-44.20 mm have been collected. Although a thorough search of all other piers in the harbour has not been possible, it is likely that the mussel is present elsewhere at similar densities. We believe these mussels represent members of a pioneer population recently established in Hong Kong.

FIG. 1. Map of Hong Kong showing the locations where *Mytilus galloprovincialis* has been recorded.

A number of morphological characteristics have been used by Wilkins et al. (1983) to identify *Mytilus galloprovincialis* and separate it from *M. edulis*. These are mantle edge colouration, shell morphometrics, the angle subtended by the ventral and ligamentary margins and, most importantly, the ratio of the length of the anterior adductor muscle scar to shell length. As the local mussel is clearly a species of *Mytilus*, these characters have been used to confirm the identity of the Hong Kong exotic.

The shell of the mussel is thin and brittle, and it appears purple-black in water but black postero-dorsally and brown antero-ventrally when dry. The shell forms a steep, tall equilateral triangle. The umbo is ventrally directed and the ventral margin nearly straight. Shell morphometrics of local specimens are compared with those given by Wilkins et al. (1983) for *Mytilus galloprovincialis* from Japan and a sample of 50 individuals of *M. edulis* obtained from Littlehampton Harbour, Sussex, U.K. (Table 1). The steep ligamentary margin of local mussels forms a large angle (53.8 ± 3.7°) with the ventral margin. The magnitude of this angle is close to that of Japanese individuals of *M. galloprovincialis* (>55°) (Wilkins et al., 1983), but different from that obtained for *M. edulis* (47.56 ± 4.24°) from Littlehampton. The shell of local mussels is wide, giving small L/W and H/W ratios. The mean value of L/H is 1.578 ±

TABLE 1. Comparisons of the angles subtended by the ligamentary and ventral margins (∠), length to height ratios (L/H) and the ratios of the anterior adductor muscle scar length to shell length (AM/L x 1000) for *Mytilus edulis* from Littlehampton, Sussex, U.K., and *M. galloprovincialis* from Japan (after Wilkins et al., 1983) and Hong Kong.

Species	∠	L/H	(AM/L) x 1000
M. edulis Littlehampton	47.56 ± 4.24	1.934 ± 0.096	118.36 ± 16.17
M. galloprovincialis (Wilkins et al., 1983)	>55	1.55 ± 0.31	74.18 ± 4.35
M. galloprovincialis Hong Kong	53.38 ± 3.69	1.578 ± 0.089	69.62 ± 16.57

0.087, comparing closely with the value of 1.55 ± 0.31 obtained for the Japanese specimens of *M. galloprovincialis* having the same length range. These figures are again different from those obtained for *M. edulis* (1.934 ± 0.096) from Littlehampton. The muscle scar patterns of the local mussel and specimens of *M. edulis* from Littlehampton are shown in Fig. 2. While both groups have consistent patterns of their own, the two are dissimilar. The ratio of the lengths of the adductor muscle scar to shell length also has been calculated. The obtained value for local mussels (69.62 ± 16.57) is very close to that seen in the Japanese mussels and that reported for the European *M. galloprovincialis* (40-95; mean = 64) (Seed, 1978), but very much lower than that reported by Wilkins et al (1983) for *M. edulis* (105.9 ± 3.9), which has a higher ratio due to a more elongate adductor (Seed, 1976). Intertidal *M. edulis* from Littlehampton have a ratio of 118.36 ± 16.17, agreeing well with the figure obtained for *M. edulis* by Wilkins et al. (1983).

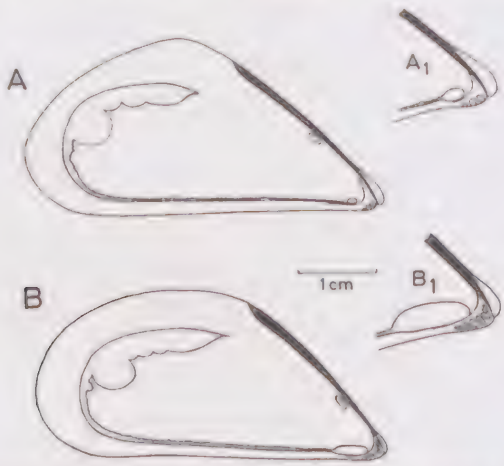

FIG. 2. Internal views of the left shell valves of A, *Mytilus galloprovincialis* from Hong Kong, and B, *M. edulis* from Littlehampton. More detailed views of the umbonal regions are shown in A_1 and B_1.

Seed (1976) concluded that a maximum temperature of 27°C is required for adult survival of *Mytilus edulis*, while *M. galloprovincialis* prefers higher temperatures. Cracium (1980) reported that mucoproteic synthetic activities in the apido-granular cells of *M. galloprovincialis* increase with temperature until 28°C, indicating an ability to reproduce (and thereby establish itself) in a warm environment. Two local specimens spawned in the laboratory after a thermal shock from 29° to 20°C, reflecting the presence of proliferating gonadal tissues at high ambient temperatures. Also, the occurrence of juveniles shorter than 20 mm in summer (July to September) suggests that reproduction, settlement and subsequent survival of spat are not hampered by the local high summer temperatures (ca. 27°C).

These pieces of evidence collectively suggest that the black mussel introduced into Hong Kong is *Mytilus galloprovincialis*. Analysis of size-frequency data obtained from a sample of *M. galloprovincialis* from North Point, Victoria Harbour, possibly indicates the presence of three constituent year classes. The smallest mode at 9 mm is likely the recruits of the current year (1984), while the two older classes were possibly recruited in the summers of 1983 and 1982. It is thus postulated that the mussel was introduced into Hong Kong sometime prior to the summer of 1982, possibly in 1981. No large, established population has so far been discovered in Hong Kong, so that settlement of planktonic larvae from nearby areas or from fouled vessels arriving in Hong Kong seems most likely. The latter mode of introduction seems probable and has been suggested for other local exotics (Morton, 1980; Huang & Morton, 1983; Huang et al., 1983; Mak et al., 1984).

The intertidal community in Victoria Harbour is dominated by the green mussel *Perna viridis* (Linnaeus) (Huang

et al., 1985). The local *Mytilus galloprovincialis* is able to thrive in the high intertidal zone (1.5 m above C.D.). Competitive interactions between these endemic and exotic species are anticipated. Possibly just as interesting, however, could be an investigation of the *Mytilus* (identified as *M. edulis*) (Anonymous, 1982) that is widely cultivated along the eastern coasts of China. The identification of *M. galloprovincialis* in southern Japan (Wilkins et al., 1983) and, now, in Hong Kong suggests that the mainland Chinese species may, at least in some southern areas, be incorrectly named.

Voucher specimens of *Mytilus galloprovincialis* from Hong Kong and *M. edulis* from Littlehampton, Sussex, U.K., have been lodged in the collections of the Museum of Zoology, The University of Michigan, Ann Arbor, U.S.A.

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NOTE ADDED IN PROOF. The status of *Mytilus galloprovincialis* is the subject of continuing discussion. Recently, Gosling (1984) concluded that *M. galloprovincialis* is but a race or subspecies of *M. edulis*. Thiriot-Quievreux (1984) concluded that, despite karyological dissimilarities between *M. edulis* and *M. galloprovincialis*, such differences are also consistent with the concept of a widespread polytypic species.

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ANODONTA WOODIANA (BIVALVIA: UNIONACEA): THE EGG REPOSITORY OF *RHODEUS SINENSIS* (PISCES: CYPRINIDAE). – Unionid bivalves have well-defined relationships with freshwater fish which serve as hosts for the parasitic glochidia larva (e.g., see Zale & Neves, 1982). In turn, unionids may act as egg repositories for certain fish, notably bitterlings (Cyprinidae: Rhodeinae), which oviposit into the mantle cavity of the mussel, where the eggs hatch and larvae develop at reduced risk from predators (Nikolsky, 1963).

Anodonta woodiana (Lea) (Unionidae: Anodontinae) is widespread is Asia and may be the only true Anodontinae in the region (Brandt, 1974; Dudgeon & Morton, 1983). *A. woodiana* glochidia encyst on a range of fish hosts (Dudgeon & Morton, 1984), including *Rhodeus sinensis* Gunther, which is common in South China (Nichols, 1943). However, the egg repository of *R. sinensis* is unknown. While *R. sinensis* does not exhibit heavy infestation of *A. woodiana* glochidia in the laboratory (Dudgeon & Morton, 1984), its suitability as a glochidial host indicates the potential for a reciprocal interaction whereby *A. woodiana* could serve as an egg repository.

This possibility was investigated by placing 28 adult *Rhodeus sinensis* (7 ♂, 21 ♀) in a 50 l tank containing seven *Anodonta woodiana* (shell length 103-123 mm, $\bar{x}$ = 115.3 mm). The animals regularly were fed powdered rat chow and 'Tetramin'; water temperatures were stable at 22°C. During a period of several weeks, the fish were seen to adopt breeding colours and the females developed ovipositors; when mature, these organs were black with a bright red band in the proximal 20% of the length. Males established and defended territories, and females were courted in a manner described by Wiepkema (1961) and Kudo (1980) for *R. amarus* and *R. ocellatus*.

The suitability of *Anodonta woodiana* as an egg repository was confirmed when, five days after the adult fish were removed, young, free-swimming *Rhodeus sinensis* emerged from the exhalant siphon of *A. woodiana*. A total of 164 young appeared over a further nine days. Thus, the period from oviposition to leaving the mantle cavity must be at least two weeks. Wiepkema (1961) reported a development period of about four weeks for *R. amarus* in *Unio* sp. as compared to two to three weeks for *R. ocellatus* in *Unio douglasiae* (Kudo, 1980).

The number of fish larvae in each *Anodonta woodiana* is unknown but, if the eggs were evenly distributed, a total of 23 fish per mussel is indicated. On the basis of subsequent survival, service as an egg repository seems to have no ill effects on *A. woodiana*.

Voucher specimens of *Anodonta woodiana* have been deposited in the British Museum (Natural History) [accession no. 2315] and the U.S. National Museum of Natural History [catalog no. 749848], and specimens of *Rhodeus sinensis* have been deposited in the Zoology Department Fisheries Collection, University of British Columbia, Vancouver, Canada [catalog no. BC 084-100].

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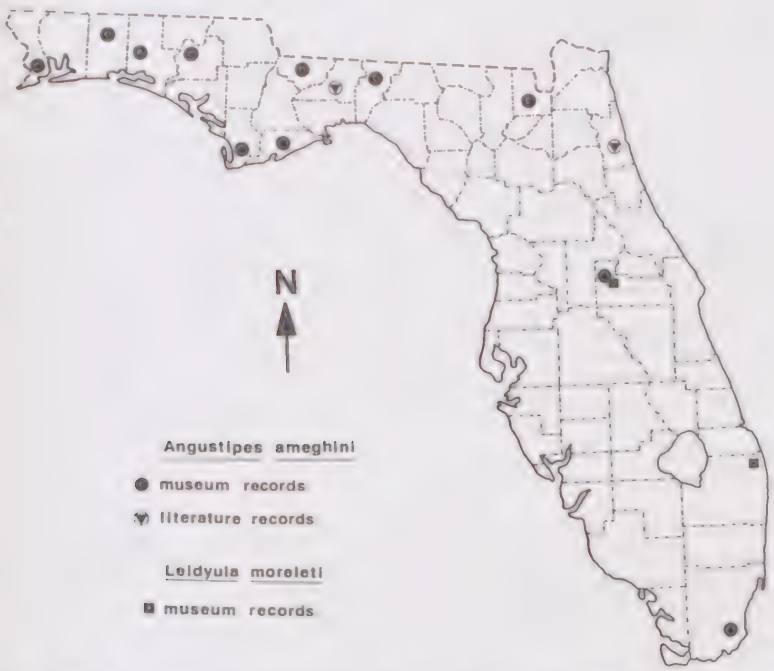
THE FOREIGN SLUGS *ANGUSTIPES AMEGHINI* AND *LEIDYULA MORELETI* (GASTROPODA: VERONICELLIDAE) IN CENTRAL FLORIDA. – Recent field work has revealed the presence of two foreign veronicellid slugs in central Florida, U.S.A.

Angustipes ameghini (Gambetta 1923). Specimens examined – Florida: Baker Co., Ray's Nursery (DPI)[1]; Escambia Co., Pensacola, 107 Southern (DPI), 7091 Kelvin (DPI), 6125 Confederate (DPI), 6950 Forshalee Dr. (DPI), Cypress Nursery (DPI); Franklin Co., 6 mi NNE of Carabelle (UF 28449)[1]; Gadsden Co., Quincy, BLT Growers (DPI); Gulf Co., Appalachicola (UF 28463); Jefferson Co., Monticello, Gro-Plant Industries Inc. (UF 40332), Q. Anglin's property (DPI); Okaloosa Co., ca. 5 mi N of Crestview (UF 30074); Orange Co., Apopka, 1912 Thor Ave. (DPI), Plymouth, Tolliver's Greenhouses (DPI), Peacock Landscape Nursery (DPI), H & T Nursery (DPI), Bryant's Nursery (DPI), Tangerine, John's Citrus Nursery (UF 40338, UF 40340, DPI), Zellwood, Florida Cactus No. 2 (UF 40341, DPI), Pokey's Citrus Nursery (DPI), Davie Lee Nursery (DPI), Zellwood Farms Mushroom Factory (UF 40343, DPI), Sec. 33 T20 R27, in fields (DPI); Walton Co., Mossy Head (UF 29982).

Angustipes ameghini, a Paraguayan slug, was first introduced to the United States in 1960, apparently simultaneously at Mobile, Alabama, and New Orleans, Louisiana (Dundee & Watt, 1961). It is recorded as established in Alabama, Mississippi, Louisiana and northern Florida (Dundee, 1974, 1977; Burch & Van Devender, 1980), but it also occurs in Cameron County, Texas (UF 34220). The anatomy is illustrated in Peterellis & Dundee (1969), and observations on the life history are given in Colvin (1962), Dundee et al. (1965) and Dundee (1977).

On 20 July 1982, a slug identified as *Angustipes ameghini* was collected in a nursery in Orange County, Florida. Specimens in the collections of the Florida State Museum, Gainesville, extend the range of *A. ameghini* in Florida from Dade, Escambia, Leon and St. Johns counties (Dundee, 1974, 1977) to Franklin, Walton, Gulf, Jefferson and Okaloosa counties (Fig. 1). Specimens housed at the Division of Plant Industry, Gainesville, further extend its range to Gadsden, Baker and Washington counties. It is likely that *A. ameghini* is distributed generally throughout the panhandle of the state.



On 26 May 1983, the distribution of *Angustipes ameghini* in Orange County was re-examined. It has now become established in the northwestern portion of the county, where it occurs in greenhouses, nurseries and grassy fields. Specimens were found under boards and potted plants, in burrows in soft soil, and inside the pots of nursery stock. Slugs enter these pots through the drainage holes at their bases.

No feeding damage was observed on the nursery plants in the area in which *Angustipes ameghini* was found to be inhabiting the rootballs of potted stock. An analysis of the stomach contents of slugs in these populations showed that they were consuming large quantities of leaf matter from vascular plants. Spores of common leaf-inhabiting fungi, *Alternaria, Cercospora, Curbularia* and *Fusarium*, also were found in the gut contents (J. Kimbrough, pers. comm.). It was not possible to determine if the leaves were decaying or living when consumed. Colvin (1962) reported that these slugs eat large amounts of both living and decayed leaves. Although the presence of these slugs in the rootball causes some mechanical damage to the roots, root tissue does not appear to be a primary source of nutrition for the slugs. Specimens maintained in captivity in Gainesville were observed to feed on the living leaves of *Epipremnum aureum*, a common nursery plant, causing moderate damage.

The egg-masses laid by *Angustipes ameghini* in Orange County conform to the description given in Colvin (1962) of spiral strands of gelatinous, oval eggs coiled with a strand of mucus. Egg masses were found both under the pots of

[1] DPI = Division of Plant Industry, Gainesville, Florida; UF = Florida State Museum, Gainesville, Florida.

nursery stock and inside the pots in the soil adjacent to the drainage holes. The number of eggs per mass of the four masses found were 33, 23, 37 and 19, with the latter two masses being those inside the pots. Newly hatched juveniles showed a pale stripe on the dorsal surface that often persisted into adulthood in the Orange County populations.

Leidyula moreleti (Crosse & Fischer 1872). Specimens examined – Florida: Dade Co., Homestead, Grant and Sons Nursery (DPI); Orange Co., Apopka, Smith Greenhouses (DPI interception from Costa Rica), Gotha, Land of Bromeliads (DPI), Tangerine, John's Citrus Nursery (UF 40339), Zellwood, Zellwood Farms Mushroom Factory (UF 40342, DPI); Palm Beach Co., Del Ray Beach (DPI interception from Puerto Rico), Jupiter, Jupiter River Park (DPI).

Leidyula moreleti is a Central American veronicellid that has been reported in the United States only from Brownsville, Texas, but frequently has been intercepted on agricultural shipments (Dundee, 1974; Burch & Van Devender, 1980). The genital anatomy is presented in Baker (1925) and Burch & Van Devender (1980).

During the re-examination of the distribution of *Angustipes ameghini*, a second species of slug was collected in Orange County and identified as *Leidyula moreleti*, a species not reported previously from Florida. Examination of veronicellid slugs in the collections of the Division of Plant Industry, Gainesville, revealed that *L. moreleti* is established also in Jupiter, east Palm Beach County (Fig. 1), where it was collected first in 1980. The Dade County record has not been verified and may represent an interception by quarantine inspectors.

In Orange County, *Leidyula moreleti* occurs in mixed populations with *Angustipes ameghini* and is found in nurseries and grassy fields. *L. moreleti* congregates with other slugs under boards and plant containers. Unlike *A. ameghini*, *L. moreleti* does not burrow and generally is not found inside the pots of nursery stock. In Palm Beach County, *L. moreleti* is found in mixed populations with *L. floridana* (Leidy), a native veronicellid. These species both were collected in beds of *Spathiphyllum* sp. and *Epipremnum aureum*. This colony was re-examined on 22 June 1983 and found to have maintained approximately the same population density as in 1980 (W. Walsh and J. Wheeler, DPI, pers. comm.).

Leidyula moreleti feeds largely on leaf material, similar to *Angustipes ameghini*. Specimens of *L. moreleti* kept in captivity in Gainesville caused considerable damage to the leaves of *Epipremnum aureum*. No feeding damage was noted on nursery stock during the survey in Orange County. However, moderate to heavy feeding damage to both host plants in Palm Beach County was observed (W. Walsh and J. Wheeler, pers. comm.), and similar damage has been noted on citrus stock in Orange County (B. Saunders, pers. comm.). In Mexico, *L. moreleti* has been found to damage the foliage of cacao plants in the state of Tabasco (J. Gutierrez, pers. comm.) and Burch (1960) has cited this species as a voracious feeder which is often destructive in gardens.

Discussion. The burrowing habit of *Angustipes ameghini* will lead to its general dispersal in Florida. The undetected presence of adult slugs or of egg masses in the rootballs of nursery plants will facilitate the spread of this species to the major horticultural areas of the state and from there to suburban and rural districts. Nurserymen specifically reported shipments to Palm Beach, Broward, Hillsborough and Volusia counties. Although *A. ameghini* does feed on leaf tissue, it does not appear to be a severe plant pest.

Leidyula moreleti does considerably more damage to leaf tissue than does *Angustipes ameghini*. A comparison of damage done by captive specimens of each species shows that *L. moreleti* destroyed six times as much foliage area as did *A. ameghini*. However, the spread of *L. moreleti* in Florida is likely to be slower than that of *A. ameghini*. Adult *L. moreleti* were not seen to burrow and were rarely found in the rootballs of nursery stock. This species has been intercepted on shipments from Costa Rica and Puerto Rico, where it was concealed by packing material, a mode of transport which could allow dispersal of the slug in Florida. However, *L. moreleti* is reported to be viviparous (Baker, 1925; Burch & Van Devender, 1980); therefore, transportation of undetected egg masses will not be a factor in its dispersal.

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THE CHROMOSOMES OF *HALIOTIS DIVERSICOLOR AQUATILIS* (ARCHAEOGASTROPODA: HALIOTIDAE).* – The Pleurotomarioidea are thought to have given rise to a number of other superfamilies belonging to the Archaeogastropoda, and the pleurotomarioids seem to have been the source of other orders as well (Knight et al., 1960). Therefore, investigations on members of the Pleurotomarioidea are very important in order to obtain information for evaluating phylogenetic relations among the various gastropod groups. Karyological information on pleurotomarioids, however, is unfortunately scarce; data on only one family, the Haliotidae, are available. Chromosome numbers of three species and subspecies of this family have been reported thus far (Table 1). In the present study, I observed the chromosome number of *Haliotis diversicolor aquatilis* to be different from that reported by Nishikawa (1962), and I also have obtained data on chromosome morphology.

TABLE 1. Chromosome numbers reported for *Haliotis*.

Species	Chromosome number	Locality	Reference
Haliotis discus discus	2n = 36 s	Shizuoka, Japan	Arai et al., 1982
H. discus hannai	2n = 36 s	Akita, Shizuoka & Ehime, Japan	Arai et al., 1982
H. diversicolor aquatilis [= *H. japonica**]	2n = 34 ♂ n = 17 I, II†	Yamaguchi, Japan	Nishikawa, 1962
H. diversicolor aquatilis	2n = 32 ♂ n = 16 I	Wakayama, Japan	Nakamura, this report

s = Somatic cell from the gill; ♂ = spermatogonium.

*Synonym used by Nishikawa (1962).

†I, II = primary and secondary spermatocytes.

Specimens used in this study were collected near the Seto Marine Biological Laboratory, Wakayama, Japan, by my colleagues, T. Imaoka and M. Ishihara, during the summers of 1982 and 1983. The chromosome preparations were made on cells from testis by the air-dry method described previously (Nakamura, 1982). Voucher specimens have been deposited in the collections of the Seto Marine Biological Laboratory, Kyoto University, Wakayama (N063083-1 & 4, N082783-1 & 2).

Haliotis diversicolor aquatilis Reeve 1846 has a diploid chromosome number of 32 (Figs. 1-3): eight pairs of metacentric chromosomes, five pairs of submetacentric chromosomes, two pairs of submetacentric or subtelocentric chromosomes and one pair of subtelocentric chromosomes (nomenclature after Levan et al., 1964). In a graduated series, the lengths of the chromosomes are slightly different from each other and no chromosome pair is remarkably larger of smaller than the others. The mean value of the total chromosome length of the diploid chromosomes from six metaphase spreads is 76.1 μm. Sixteen bivalents were observed at male meiotic diakinesis (Fig. 2) and no abnormal chromosome behavior was observed during meiosis, as I previously reported for neritid sex chromosomes, which appeared heterochromatic (Nakamura, 1984). As previously pointed out, there are some faulty observations in Nishikawa's report, which resulted from the techniques of preparation he used (Patterson, 1967; Nakamura, 1984). I suspect the difference in chromosome number of *H. diversicolor aquatilis* that Nishikawa reported and I observed are due to artifacts in his preparation. Otherwise, it may be due to an intraspecific polymorphism of chromosome number, as has been found in a neritid species, *Dostia violacea* (Nakamura, 1984), or reported in a European muricid, *Thais* (= *Purpura*) *lapillus* (Staiger, 1954). The results obtained from *H. discus discus* and *H. discus hannai* (Arai et al., 1982) are different from those of *H. diversicolor aquatilis* examined here, both in morphology and in number of chromosomes. The former two are reported to have a chromosome number of 2n = 36 and a karyotype consisting of 10 pairs of metacentric and eight pairs of submetacentric chromosomes. The most remarkable difference in the karyotypes of *H. diversicolor aquatilis* and *H. discus* is that *H. discus* has no typical subtelocentric pair of chromosomes corresponding to chromosome pair 16 of *H. diversicolor aquatilis*. Two of the eight chromosome pairs described as submetacentric (the third and fourth smallest, chromosome pairs 15 and 16) appear to be subtelocentric and may correspond to chromosome pairs 14 and 15 of *H. diversicolor aquatilis*.

A general stability with regard to chromosomal condition has been suggested for most molluscan groups (Burch, 1961; Patterson, 1967). Although the information is available only from two species of *Haliotis* so far, my observation of differences in number and shape of chromosomes within this genus may be phylogenetically significant. Further karyological studies on other species will enable us to know how extensively the chromosomal variability exists in this family.

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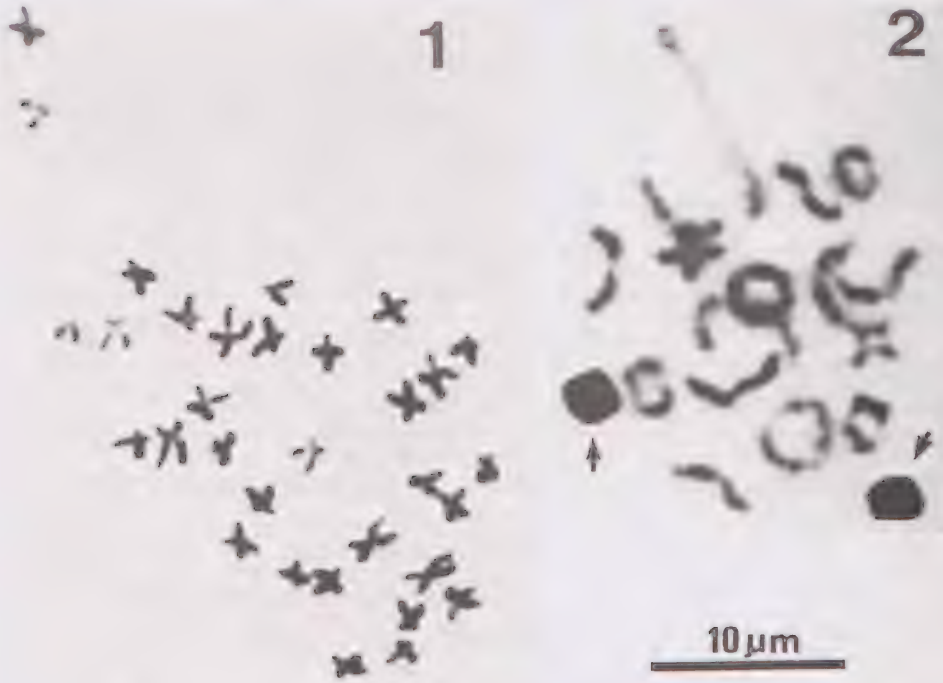
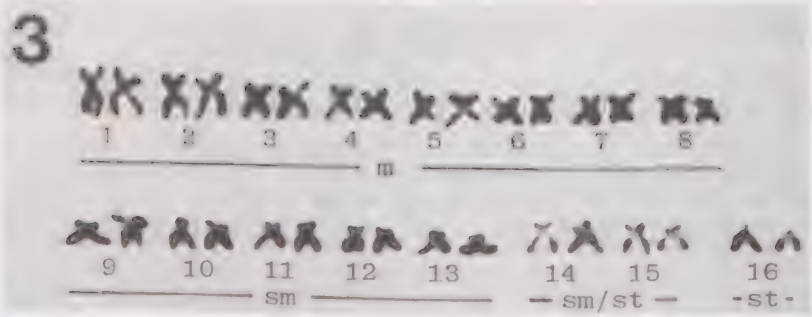
*Contribution from the Seto Marine Biological Laboratory, No. 701.





FIGS. 1-3. Chromosomes of male *Haliotis diversicolor aquatilis*. FIG. 1. Mitotic metaphase chromosomes from a testicular cell, 2n = 32. FIG. 2. Diakinesis of a primary spermatocyte, n = 16. Arrows indicate a spermatid. FIG. 3. Karyotype constructed from the chromosomes shown in Fig. 1.

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FRESHWATER MUSSELS (PELECYPODA: UNIONIDAE) OF THE MAJOR TRIBUTARIES OF THE ST. CLAIR RIVER, MICHIGAN. – Western Lake Erie, Lake St. Clair, and the associated tributary streams harbor the richest freshwater mussel fauna in the St. Lawrence River drainage (Goodrich & van der Schalie, 1932). Although some recent surveys have contributed to our knowledge of the current fauna (e.g., Clarke, 1973; Clark, 1977; Strayer, 1979, 1980), there is a paucity of published data available for several major drainages in the region. Furthermore, since many of the freshwater mussels listed as rare, threatened or endangered by the Michigan Department of Natural Resources (1983) are known from this area, further survey work is necessary to determine the present status of these faunal elements.

Study area and methods. To ameliorate our understanding of current freshwater mussel distributional patterns, the Black (including Elk and Mill creeks), Pine and Belle rivers (which are tributary to the St. Clair River) were surveyed during the summer and fall of 1982 and 1983. The drainage basin is predominantly level glacial lake plain underlain by silty loam and sandy loam soils. Land use in this region is primarily agricultural (Hull, 1978). At the sampled localities, these hardwater rivers rarely reached widths of 15 m with low-level water depths of less than 2 m.

Twenty-seven sites harbored live freshwater mussels (Fig. 1). Collections were made by handpicking the shallows with the aid of waterscopes. Identifications were made according to Burch (1975) and representative specimens placed in the Museum of Zoology, The University of Michigan.

Collecting stations. 1) Black R. at Deckerville Rd. (S25,R14E,T13N; Sanilac Co.); 2) Black R. at Forester Rd. (S12,R14E,T12N; Sanilac Co.); 3) Black R. at Custer Rd. (S19,R15E,T12N; Sanilac Co.); 4) Black R. at Church Rd. (S4,R15E,T11N; Sanilac Co.); 5) Black R. at Washington Rd. (S15,R15E,T11N; Sanilac Co.); 6) Black R. at French Line Rd. (S23,R15E,T11N; Sanilac Co.); 7) Black R. at Aitken Rd. (S7,R16E,T10N; Sanilac Co.); 8) Black R. at Galbraith Line Rd. (S29,R16E,T9N; Sanilac Co.); 9) Black R. at Comstock Rd. (S17,R16E,T8N; St. Clair Co.); 10) Black R. at Norman Rd. (S29,R16E,T8N; St. Clair Co.); 11) Black R. below 'Ford' Dam (S8,R16E,T7N; St. Clair Co.); 12) Black R. at Wadhams Rd. (S2,R16E,T6N; St. Clair Co.); 13) Elk Cr. at Stilson Rd. (S16,R14E,T10N; Sanilac Co.); 14) Elk Cr. nr. Fitch Rd. (S31,R15E,T11N; Sanilac Co.); 15) Elk Cr. at Walker Rd. (S17,R15E,T11N; Sanilac Co.); 16) Mill Cr. at Brown City Rd. (S10,R12E,T8N; Lapeer Co.); 17) Mill Cr. at Hwy. M-19 (S36,R14E,T8N; St. Clair Co.); 18) Pine R. at Fargo Rd. (S23,R15E,T7N; St. Clair Co.); 19) Pine R. at Bryce Rd. (S24,R15E,T7N; St. Clair Co.); 20) Pine R. at Hwy. M-21 (S31,R16E,T7N; St. Clair Co.); 21) Pine R. at Dove Rd. (S21,R16E,T6N; St. Clair Co.); 22) Pine R. at Frith Rd. (S9,R16E,T5N; St. Clair Co.); 23) Pine R. at Mitchell Rd. (S15,R16E,T5N; St. Clair Co.); 24) Belle R. at Capac Rd. (S9,R13E,T6N; St. Clair Co.); 25) Belle R. at Hwy. M-19 (S35,R14E,T6N; St. Clair Co.); 26) Belle R. at Hwy. M-25 (S32,R15E,T5N; St. Clair Co.); 27) Belle R. at Indian Trail Rd. (S15,R16E,T4N; St. Clair Co.).

Results and Discussion. Twenty-five species of freshwater mussels were collected live from the Black, Pine and Belle river drainages (Table 1). Nine mussels, *Actinonaias carinata, Dysnomia torulosa, D. triquetra, Lampsilis fasciola, Obovaria subrotunda, Proptera alata, Ptychobranchus fasciolare, Truncilla truncata* and *Villosa fabalis* were found to be rare. Conversely, mussels found to be abundant included *Amblema plicata, Anodonta grandis, Lampsilis radiata siliquoidea* and *Lasmigona complanata*.

From this investigation it is apparent that the Black, Pine and Belle rivers of southeastern Michigan harbor a diverse array of freshwater mussels. The sites with high diversity (Stations 7, 15 and 22) had very similar substrates, i.e., deep,

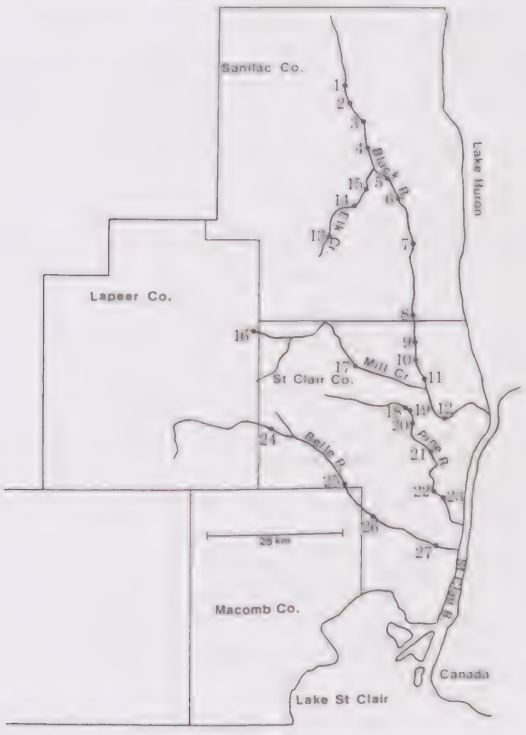

FIG. 1. Map of collecting stations on the St. Clair River drainage, southeastern Michigan.

TABLE 1. List of mussel species found live at each station in the St. Clair River drainage, southeastern Michigan.

Species	Station number																									
	Black River												Elk Creek			Mill Creek		Pine River						Belle River			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Actinonaias carinata (Barnes)							R																				
Alasmidonta calceolus (Lea)													C	R	R					R							
Alasmidonta marginata Say				C			R		R	C					R												R
Amblema plicata Say		R	R		A	A	A	R		R			A	A	A					R	C	C					R
Anodonta grandis Say	A	A	A	C	R	R	R						A		C		R		R		C	C	C	C	R	R	
Anodontoides ferussacianus (Lea)	R		R	R		R							A			R	R	R	R						R		
Dysnomia torulosa (Rafinesque)***							R								R												
Dysnomia triquetra (Rafinesque)**																						R					R
Elliptio dilatata Rafinesque						C	C													A			R				
Fusconaia flava (Rafinesque)			R		A	A	C						C	C	A							R	R				
Lampsilis fasciola Rafinesque*															R												
Lampsilis ovata (Say)						R						R		R	R		R				R	R	R		R		R
Lampsilis radiata siliquoidea (Barnes)		A	A	R	C	C	C	R	R	R	C		R		C						C	A	A		R	C	C
Lasmigona complanata (Barnes)	C	A	A	A	A	A	C	A	C	C		R	A	C	C		R				A	C	R		R	R	C
Lasmigona compressa (Lea)	R		R					R					R								R	R	R			R	
Lasmigona costata (Rafinesque)			R	R	R	C	A					R			C						R	C				C	R
Leptodea fragilis (Rafinesque)											C	C										R	R				
Obovaria subrotunda (Rafinesque)**																						R					
Pleurobema cordatum (Rafinesque)					R	A	C								R						R						
Proptera alata (Say)																						R					
Ptychobranchus fasciolare (Rafinesque)							R								R								R				
Strophitus undulatus (Say)				R		R	R								R							R			R	C	C
Truncilla truncata Rafinesque												C															
Villosa fabalis (Lea)***																					R	R	R				
Villosa iris (Lea)														R						C		A			R	R	

*Rare, **threatened, or ***endangered, as listed by the Michigan Department of Natural Resources (1983).
Abbreviations: A (abundant) = >5 mussels/man hr.; C (common) = 1-5 mussels/man hr.; R (rare) = <1 mussel/man hr.

coarse sand and gravel. Many of the Michigan-listed unionids (Michigan Dept. Nat. Resources, 1983) are known to inhabit gravel bars, where they are often found deeply buried (van der Schalie, 1938; Parmalee, 1967; Johnson, 1978). Throughout lotic ecosystems, this particular type of substrate is fast disappearing due to increased siltation from modern agricultural practices, channelization and dam construction for flood control and power generation (Stansbery, 1970). If the present fauna is to be preserved, a concerted effort must be initiated to preserve this type of habitat.

The proximity of the study sites to Lake St. Clair and Lake Erie undoubtedly contributes to the high diversity of freshwater mussels. Of the species encountered in this study that are considered rare, threatened or endangered (Table 1), all five have been found in Lake Erie or Lake St. Clair (Goodrich & van der Schalie, 1932). It is obvious that the closer a particular site is to a source of colonizing individuals, the greater the likelihood that larval mussels will reach that site by way of fish potentiated phoresis. However, this colonizing ability is severely hampered by dam construction. In the upper Black River drainage, mussel populations are virtually isolated from populations in the lower drainage and Lake St. Clair by 'Ford' Dam (St. Clair Co.). If the upper drainage populations were decimated by either a natural or an anthropogenic perturbation, it would be impossible for recolonization to occur from downstream populations. Given this possibility, it is important to note that *Dysnomia torulosa*, considered rare and endangered throughout its range (Stansbery, 1970), was found exclusively in the upper Black River drainage above 'Ford' Dam.

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MISCELLANEA

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COMMENTS ON THE STATUS OF RECENT MEMBERS OF THE GENUS *MYTILOPSIS* (BIVALVIA: DREISSENIDAE)

Dan C. Marelli[1] and Susan Gray

The bivalve family Dreissenidae includes two extant genera, *Dreissena* and *Mytilopsis*, the species of which are mytiliform, byssate and epifaunal, and are capable of adapting to wide variations in salinity. *Dreissena* Beneden 1835 (type-species by monotypy: *Mytilus polymorphus* Pallas 1771) is represented by a single species restricted to Great Britain and continental Europe, whereas nominal species of *Mytilopsis* Conrad 1858 (type-species by subsequent designation of Dall (1898): *Mytilus leucophaetus* Conrad 1831) occur in northwestern Europe, western Africa, eastern North America, Central America, South America and in three localities in Asia. The taxonomy of *Mytilopsis* is confused because of a profusion of synonyms, and because the systematic relationships within *Mytilopsis* are unclear. Therefore, in this paper, we review the taxonomy and comment on the systematic status of the species of *Mytilopsis*.

Pallas (1771) described the first known dreissenid as *Mytilus polymorphus* because of its superficial similarity to marine mussels. Beneden (1935) subsequently established the generic name *Dreissena* for *M. polymorphus* (see Keen, 1969, for summary). Gray (1840) later erected a new superfamily, Dreissenacea, and a new family, Dreissenidae, to include *Dreissena*, which at that time comprised four nominal species in Europe, Africa and North America. Conrad (1858) recognized differences in the character states of shells of *D. polymorpha* and the American dreissenids, and erected the genus *Mytilopsis* for the American group. The Dreissenidae were still considered to be phylogenetically closely related to the Mytilidae for some time (e.g., Dall, 1898; Maury, 1920). Presently, however, the Dreissenidae are placed in the subclass Heterodonta, order Veneroida, on the basis of the anatomical features of Recent dreissenids and the conchological character states of fossil members (Yonge & Campbell, 1968; Keen, 1969; Morton, 1970). The superficial similarity between the Mytilidae and the Dreissenidae is therefore the result of convergent evolution, rather than close phylogenetic relationship (Yonge & Campbell, 1968; Keen, 1969, 1971; Morton, 1969, 1970). The Dreissenacea are considered to be most closely related to the Corbiculacea, and it is probable that the dreissenids evolved from a corbiculacean ancestor (Morton, 1970).

The Dreissenidae probably originated during the Eocene, in the Ponto-Caspian Basin (Keen, 1969; Morton, 1970; Archambault-Guezou, 1976). Occasional reference has been made to Cretaceous dreissenids from Europe and the Americas (Woods, 1900; Gardner, 1916; Stephenson, 1923; Kauffman, 1973), but these fossils have subsequently proven to be examples of aberrant mytilids (Soot-Ryen, 1969). At the time of dreissenid evolution, migrational routes through shallow, warm seas from Europe to the Americas were non-existent (Kauffman, 1973). Therefore, the ancestors of *Mytilopsis* probably were introduced to the New World by rafting on buoyant vegetation. This mode of dispersal is favored since a similar mode, introduction by shipping, has been implicated in modern continental introductions of several species of *Mytilopsis* (Morton, 1981; Marelli & Gray, 1983).

The systematic relationships among dreissenid genera are unclear. Some authors have postulated a sole ancestor in the extinct genus *Congeria* Partsch 1835 for *Dreissena* and *Mytilopsis* (Morton, 1970). But, on the basis of shell morphologies, it appears that *Mytilopsis*

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and *Congeria* are more closely related to each other than either is to *Dreissena*. In fact, *Mytilopsis* has been considered to be a junior synonym of *Congeria* (e.g., Dall, 1898), or a subgenus of *Congeria* (e.g., Pilsbry, 1911; Hertlein & Hanna, 1949). Recent workers, however, treat *Mytilopsis* and *Congeria* as distinct genera, and agree that *Mytilopsis* is the sole extant dreissenid genus occurring in the New World (Keen, 1969; Morton, 1970).

Until recently, *Mytilopsis* was considered to include nine extant species. Despite an early plea by Dall (1898), no workers have attempted a taxonomic revision of this group since that of Küster (1889), which was somewhat incomplete. Recent work by Marelli & Gray (1983, and in preparation) based on conchological character states suggests that five of the nine species are valid. These are: *M. africana* (Beneden 1835) of the eastern Atlantic Coast from Algeria to Gabon; *M. leucophaeta* (Conrad 1831) of the Gulf of Mexico and western Atlantic coasts from Massachusetts, U.S.A., to Tampico, Mexico (and introduced into northwestern Europe); *M. sallei* (Récluz 1849) of the West Indies and the Caribbean Coast of Central and South America from Yucatan to Venezuela and in southern peninsular Florida, U.S.A. (also reportedly introduced into Fiji, Japan and northeastern India); *M. adamsi* Morrison 1946 from western Panama; and *M. trautwineana* (Tryon 1866) of the eastern Pacific Coast in Ecuador and Colombia (Morrison, 1946; Hertlein & Hanna, 1949; Olsson, 1961; Keen, 1971; Morton, 1981; Marelli & Gray, 1983; T. Habe, pers. comm.; and museum records examined by the authors).

Morton (1981) has suggested that *Mytilopsis allyneana* Hertlein & Hanna 1949 is a synonym of *M. sallei*, and hence that *M. sallei* is found in Fiji, eastern India and Orido Bay, Japan. Marelli & Gray (1983), following Morton (1981), included *M. allyneana* as a synonym of *M. sallei*. However, in examining specimens more critically, it appears that *M. allyneana* is a synonym of *M. adamsi*, and is undoubtedly a Pacific representative. Morton (1981) postulated that *M. sallei* was introduced into Fiji via ships travelling from the Atlantic Ocean through the Panama Canal, and was subsequently carried by shipping to eastern India. Dall (1898), however, reported a species of *Congeria* from the Viti Isles (Fiji) prior to the opening of the Panama Canal in 1914. Additionally, the British Pacific Steamship Navigation Company ran mail steamships between Panama and Australia during several time periods in the 1860s and 1870s, apparently using Fiji as a port (Robinson, 1907; Coulter, 1942). Steamships leaving Panama were coaled on the island of Taboga, where fresh water (and presumably brackish water) is in abundance (Robinson, 1907). Taboga is a member of the Perlas Islands, the largest of which, San José, is the type locality for *M. adamsi* (Morrison, 1946). During the late 19th century, British ships carried indentured servants and repatriates between eastern India and Fiji (Coulter, 1942). Therefore, it is likely that *M. adamsi* was introduced from Panama to Fiji in the late 19th century, and subsequently to India, via British shipping.

On the basis of conchological character states, *Mytilopsis* may be divided into two distinct species groups. Species-group A, comprising *M. adamsi* and *M. leucophaeta*, is characterized by relatively long, low and wide shells with nearly straight ventral margins, and slightly convex dorsal margins. The shell interiors of members of this species group exhibit relatively short septa, and therefore the lateral apophyses are more conspicuous (see Marelli & Gray, 1983). In actuality, the apophyses of species-group A members are less well developed and more closely associated with the septum than are those of species in group B (Fig. 1) (see Marelli & Gray, 1983). Species-group B comprises *M. africana, M. sallei* and *M. trautwineana*. Species in this group are higher and less wide than those of group A, and possess shells which usually are strongly concave ventrally and sharply convex dorsally. Shells of this species group also are more sharply pointed anteriorly than are those of species-group A. The shell interiors of members of species-group B possess long septa which partially obscure the apophyses. The apophyses are not closely associated with the septum, and are well developed in this group, often being sharply pointed posteroventrally and having a hooked appearance (Fig. 2). *M. allyneana* clearly belongs to species-group A, and is indistinguishable from *M.*

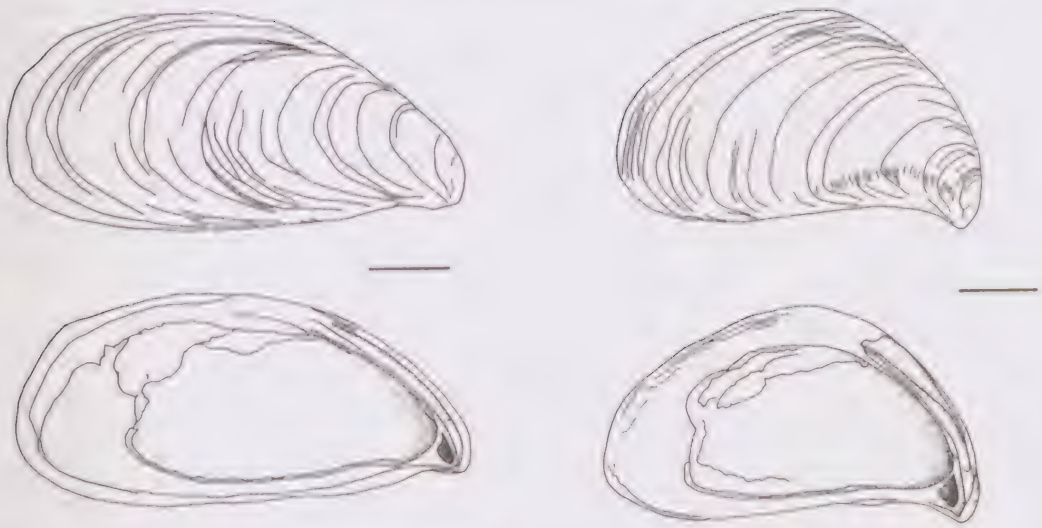

FIG. 1. Interior and exterior views of valves of *Mytilopsis leucophaeta*, an example of species-group A. Specimen from Student Lake, Miami, Florida, U.S.A. (U.S. National Museum [USNM] 818345). Scale bar = 2 mm. FIG. 2. Interior and exterior views of valves of *M. sallei*, an example of species-group B. Specimen from Laguna Bacalar, Quintana Roo, Mexico (USNM 818346). Scale bar = 2 mm.

adamsi based on conchological character states. *M. allyneana* is therefore treated herein as a junior subjective synonym of *M. adamsi*.

It is clear that *Congeria* and *Mytilopsis* are closely related, based on the presence of shared derived characters (Table 1), and that these genera represent a distinct evolutionary line from *Dreissena* within the Dreissenacea (Fig. 3). The major distinction between these evolutionary lines is the condition of the hinge plate and its associated structures (see Morton, 1970). In *Mytilopsis* and *Congeria*, these structures exist in a derived condition, whereas *Dreissena* displays the ancestral condition. Specialization of the hinge structure is in an early state in

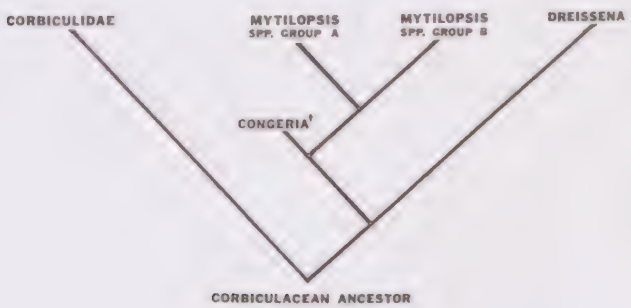

FIG. 3. Phylogram showing probable relationships between genera of Dreissenidae, and species groups of *Mytilopsis*.

TABLE 1. Relative conchological character states of dreissenacean genera.

Conchological characters	Character states by genus				
	Dreissena s.l.	*Dreissena s.s.*	*Congeria*	*Mytilopsis* spp. A	*Mytilopsis* spp. B
Exterior					
Shell shape	Long, moderately high, wide	Long, moderately high, wide	Rhomboidal to mytiliform	Long, low, wide	Long, high, narrow
Ventral margin	Straight	Straight	Straight to strongly convex	Nearly straight to weakly concave	Moderately to strongly concave
Dorsal margin	Nearly straight to strongly convex	Moderately convex	Moderately to strongly convex	Broadly convex	Strongly convex
Shape of anterior region	Broadly rounded to narrowly rounded	Narrowly rounded	Broadly rounded to sharply pointed	Well rounded to bluntly pointed	Bluntly pointed to sharply pointed
Shape of posterior region	Quadrate to broadly oval	Broadly oval	Broadly oval to quadrate	Broadly oval to somewhat quadrate	Broadly oval
Interior					
Postion of posterior muscle scars	Entirely posterior of nymph	Entirely posterior of nymph	Entirely posterior of nymph	Entirely posterior of nymph	PRM reaches posterior limit of nymph
Shape/size of posterior muscle scars	Approximately equal in size, compact to elongate	Approximately equal in size, PRM scar elongate	Approximately equal in size, PA often larger	Approximately equal in size, PRM scar elongate	Approximately equal in size, PRM scar elongate
Condition of pallial line	Entire to deeply sinuate	Entire	Entire	Entire	Entire
Appearance of inner surface of shell	Unknown	Unknown	Unknown	Porcellaneous except pallial line and muscle scars	Porcellaneous except pallial line, muscle scars and extrapallial region
Position of anterior muscle scars	On hinge plate or on septum	Both on septum	AA on septum AR on apophysis	AA on septum AR on apophysis	AA on septum AR on apophysis
Condition of septum	Obsolescent to well developed	Well developed	Well developed	Well developed, wide, rounded anteriorly	Well developed, pointed anteriorly
Condition of apophysis	Absent	Absent	Present and weakly developed	Present, well developed, close to septum	Present, well developed, well separated from septum
Ligament	Internal, < ½ to ½ distance to posterior margin	Internal, ½ distance to posterior margin	Internal, nearly ½ to ½ distance to posterior margin	Internal, < ½ distance to posterior margin	Internal, to ½ distance to posterior margin
Condition of hinge teeth	Present and rudimentary to absent	Absent	Nearly absent to absent	Absent	Absent
Secondary hinge teeth	Absent	Absent	Absent	Present and well developed	Present and moderately developed

AA = Anterior adductor; AR = anterior retractor; PA = posterior adductor; PRM = posterior retractor muscle.

Congeria, whereas in *Mytilopsis* these structures exist in a more specialized condition, or a more derived state. Conchological character states in *Mytilopsis* species-group A members more closely resemble those of *Congeria* than do the states of the homologous characters in members of species-group B (Table 1). Thus, group A (*Mytilopsis adamsi* and *M. leucophaeta*) may represent the more ancestral species group in *Mytilopsis*.

The foregoing interpretations should provide further insight into the interrelationships among dreissenid genera and among species of *Mytilopsis*. Work in this area has been hampered by taxonomic uncertainties, but, with these resolved, more detailed consideration of systematic, evolutionary and biogeographic questions may proceed.

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Malacological Review, 1985, 18: 123-124

OBITUARY
WILLIAM J. CLENCH
October 24, 1897 - February 22, 1984

Dr. William J. Clench was a born communicator, naturalist/collector, systematist/curator, and zoogeographer. Had he written his autobiography, he would no doubt have recounted stories of vacations at Round Top Farm, Cairo, New York, where, during his early childhood, he gathered everything that moved including insects and snails and amused the guests with his finds. He continued in this vein all his life. Those who knew him well remember him as a great story teller, one who thoroughly enjoyed his own jokes, who was a prolific letter writer and to whom the arrival of the morning mail was always an event.

Bill was born in Brooklyn, New York, in 1897 but his family moved to Dorchester, Massachusetts, in 1906. During his early years in the Dorchester public schools, he was an all-around naturalist, and, according to his father, knew the names of the local trees and common insects. In 1913, he entered the Huntington School in Boston. It was here he met Kendall Foster and the two became fast friends for, as noted in the school yearbook, they "would rather discuss bugs than eat." During this period the "triumvirate" (Clench, Foster, and Sheldon Remington, a Dorchester neighbor and lifelong friend) roamed the Fenway, the Blue Hills and the local beaches collecting bugs and shells. After a good trip, they headed for the Boston Society of Natural History (BSNH) to see Charles W. Johnson, the curator of insects and mollusks. Johnson enthused over their collections, helped them with their identifications, introduced them to the literature and, according to Bill, made them feel as though their visit was the most important thing that had happened that day. Johnson also introduced the boys to the Boston Entomological and Boston Malacological Clubs, to Nathan Banks in the Entomology Department and to William F. Clapp in the Mollusk Department at the Museum of Comparative Zoology (MCZ). Bill idolized and emulated C.W. Johnson and later, as curator of mollusks at the MCZ, his interest in and encouragement of young malacologists, whether student, professional or amateur, stemmed from his experience at the BSNH. After Johnson's death in 1932, Bill checked his unpublished manuscript "List of Marine Mollusca of the Atlantic Coast from Labrador to Texas", which was published in 1934. In 1941, Bill named *Johnsonia*, Monographs of Western Atlantic Marine Mollusks, in Johnson's honor.

Michigan State College, East Lansing, Michigan, was Bill's beloved undergraduate school. Here he majored in entomology, but also found time to be treasurer of his class and otherwise active in student

affairs as well as playing saxophone in a student dance orchestra. At the same time, he continued his interest in mollusks and often went down to Ann Arbor to see Calvin Goodrich and Bryant Walker at the Museum of Zoology. In the summer of 1921, as a graduation present from his father and at the suggestion of William Clapp, Bill went on a collecting trip to Sanibel Island, at that time a little-known island off the west coast of Florida. This was his introduction to the "tropics" and it made a lasting impression. In the fall he returned to Dorchester and Cambridge to study entomology under William Morton Wheeler at Harvard University, receiving his MS in February 1923.

Following this, he changed directions, returned to Michigan, and entered The University of Michigan Graduate School to study mollusks under Goodrich and Walker, though he never lost his interest in entomology. Contributing factors to this change were, no doubt, his trip to Sanibel Island, renewed association with Johnson and Clapp while at Harvard, the offer of a Hinsdale Fellowship from The University of Michigan, plus the fact that Julia Helmich (whom he married in 1924) lived in East Lansing, Michigan.

As a graduate student in the Museum of Zoology, Bill went on his first real expedition to collect freshwater mollusks in 1923. A second trip in 1924 with Sheldon Remington set the pattern for his lifelong interest in land and freshwater mollusks.

In 1925, his Ph.D. degree unfinished, Bill left Ann Arbor to accept the position of custodian of collections at the Kent Scientific Museum in Grand Rapids, Michigan, and a year later assumed the curatorship of mollusks at the Museum of Comparative Zoology at Harvard University, a position he retained until his retirement in 1966.

Bill was a natural curator and, particularly during his early years, put a great deal of time and effort into enlarging the collection and strengthening its scientific value. His curatorial procedures gave the collection the reputation among malacologists of being the easiest one to use and the department a rather special place to work.

When he arrived at the Museum of Comparative Zoology in 1926, the mollusk collection was housed in one room on the fifth floor. It contained 45,260 catalogued lots and about 35,000 lots of unworked material. There was no departmental library. The following year, Dr. Barbour, the Director, floored over the exhibit galleries on the fourth floor of the east wing of the museum and in 1928 the Mollusk Department moved into new quarters. A flood of material immediately started pouring into the department as a result of Bill's field work (he made over 40 trips and 2,000 stations and every student had the opportunity of working with him in the field), his encouragement of amateurs who then contributed material to the collection, his active exchange program and his ability to seek and obtain for the MCZ important old collections that were no longer appreciated in their parent institutions. During his tenure as curator, Bill increased the size and scientific value of the collection more than ten-fold, placing it among the four most important malacological research collections in the world. At the time of his retirement, the department occupied five large and two small rooms and was "bursting at the seams". Over 260,000 lots had been catalogued and over 12,000 species added to the collection. But, with all this, so much had come in that there was still an equivalent amount of unworked material. In addition, the department, which had been totally inactive from 1922 to 1926, became an outstanding center for training in malacology. Included among Dr. Clench's graduate students were: Harald Rehder, Henry Russell, Tucker Abbott, Isabel Perez Farante, Thomas Pulley, Ruth Turner, Yoshio Kondo, Edward Michelson, Donald McMichael, Arthur Merrill, J. Lockwood Chamberlain, Robert Robertson, Joseph Rosewater, Arthur Clarke, Joseph Vagvolgyi, Kenneth Boss, Vida Kenk and José Stuardo. In addition to these formal students were a host of others, Harvard undergraduates and malacologists from other institutions, who came to work with him, under his guidance or simply to use the collections. As a result of his enthusiasm for mollusks, his interest in people, and his ability to communicate at all levels (verbally or by letter), he was the idol of amateurs everywhere.

Dr. Clench published at least 420 scientific papers; was the founder and editor of *Johnsonia*, Monographs of Western Atlantic Marine Mollusks, and *Occasional Papers on Mollusks*, published by the department. He was a special editor for Webster's *New International Dictionary, Encyclopedia Americana, World Book, McGraw-Hill Encyclopedia of Science and Technology*, as well as being associate editor on the boards of numerous molluscan journals. He belatedly received his Ph.D. from The University of Michigan in 1953, the same year he received an honorary D.Sc. from his alma mater, Michigan State University. After his retirement, he was appointed Adjunct Professor of Zoology at Ohio State University, Columbus, and continued field work in freshwater mollusks with Dr. David H. Stansbery and his students.

Mollusks and the MCZ were Bill's life – he was one of the founders and third president of the American Malacological Union, and he was president of the Boston Malacological Club several times, seeming always to hold some office, and seldom missed a meeting. He gave freely of his time and talents to novices and specialists alike, and he always made visitors to the department welcome. He was an honorary member of several scientific institutions and numerous shell clubs, and he was honored during the U.S. Bicentennial Celebrations as one of Boston's 200 Distinguished Citizens, a tribute to his scientific achievements, interest in people, and ability to communicate.

RUTH J. TURNER

NEWS AND ANNOUNCEMENTS

* * * * *

UNITAS MALACOLOGICA. – *Unitas Malacologica* is an international organization of malacologists and malacological societies whose goal is to support malacological research throughout the world and to regularly organize international malacological Congresses. The originally European society, founded in 1962 in London, was changed into a more broadly international organization in 1977 and now has more than 200 members all over the world. Its legal domicile is Basle, Switzerland. The annual subscription is 20 Swiss francs. This membership fee includes the Proceedings of the Congresses, held every third year. The last Congress was held in Budapest, Hungary, in 1983. The next International Malacological Congress will be held in Edinburgh, Scotland, in 1986.

Questions and applications with respect to membership should be sent to the Secretary, Dr. Oliver E. Paget, Natural History Museum, Burgring 7, A-1014 Vienna, Austria.

FIRST COURSE ON MEXICAN NON-MARINE MALACOLOGY. – The First Course on Mexican Non-Marine Malacology was given at the Universidad Nacional Autonoma de México's Los Tuxtlas Tropical Biological Station during October and November 1984. The course included lectures on taxonomy, morphology, zoogeography, ecology, physiology and genetics, as well as laboratory (practical) sessions and field trips. Prof. J.B. Burch was the lecturer for the course and Dr. Alejandro Cruz-Reyes was the organizer and coordinator.

A sequel to the course is projected for 1986. For further information, write to Dr. Alejandro Cruz-Reyes, Instituto de Biología, Universidad Nacional Autonoma de México, Apartado Postal 70-153, 04510 México, D.F., México.

THE INSTITUTE OF MALACOLOGY held its annual meeting on 28 July 1985 in Kingston, Rhode Island, U.S.A. Members present were Melbourne R. Carriker (presiding), Kenneth J. Boss, George M. Davis, James W. Nybakken, Robert Robertson, Clyde F. E. Roper and W. R. Russell-Hunter.

AMERICAN MALACOLOGICAL UNION ANNUAL MEETING, 1985. – The 51st annual meeting of the American Malacological Union was held on the campus of the University of Rhode Island, Kingston, Rhode Island, U.S.A., from 28 July to 2 August 1985. Dr. Melbourne R. Carriker was the presiding officer and Dr. Robert Bullock was the local representative.

KOREAN SOCIETY OF MALACOLOGY. – Because of their increasing interest in mollusks, Korean biologists have now formed the Korean Society of Malacology. Several meetings already have been held, and others are planned. Interested parties should contact the Secretary of the Society, Dr. Pyung-Rim Chung, Institute of Tropical Medicine, Yonsei University, C.P.O. 8044, Seoul, Korea.

MEETING OF THE SOCIETY FOR EXPERIMENTAL AND DESCRIPTIVE MALACOLOGY. – The 1985 annual business meeting of the Society for Experimental and Descriptive Malacology will be held in December 1985 in Ann Arbor, Michigan, U.S.A. For further details, contact Dr. J.B. Burch, Secretary-Treasurer of the Society, P.O. Box 3037, Ann Arbor, Michigan 48106, U.S.A.

THE 1986 ANNUAL MEETING OF THE SOCIETY FOR EXPERIMENTAL AND DESCRIPTIVE MALACOLOGY will be held in Ann Arbor, Michigan, U.S.A., in January 1986. For further information, contact Dr. J.B. Burch, Society for Experimental and Descriptive Malacology, P.O. Box 3037, Ann Arbor, Michigan 48106, U.S.A.

THE 1986 ANNUAL MEETING OF THE INSTITUTE OF MALACOLOGY will be held in Monterey, California, U.S.A., just prior to the annual meeting of the American Malacological Union. For further details, contact Dr. Melbourne R. Carriker, President of the Institute of Malacology, c/o College of Marine Studies, Field Station, University of Delaware, Lewes, Delaware 19958, U.S.A.

AMERICAN MALACOLOGICAL UNION MEETING, 1986. – The 52nd annual meeting of the American Malacological Union will be held in Monterey, California, from July 1 to July 6, 1986, at the new Sheraton Hotel. For further information, contact Dr. James W. Nybakken, Moss Landing Marine Laboratories, Box 223, Moss Landing, California 95039, U.S.A.

NINTH INTERNATIONAL MALACOLOGICAL CONGRESS, EDINBURGH, 31 AUGUST - 6 SEPTEMBER 1986. – The Ninth International Malacological Congress will be held in Edinburgh in 1986, from 31 August to 6 September, and all malacologists are cordially invited. For further details contact the Congress Office, Royal Scottish Museum, Edinburgh, Scotland, EH1 1JF, U.K. Accommodation for participants will be provided at the Pollock Halls of Residence, University of Edinburgh (single rooms only) and at a variety of hotels near the city centre. The scientific programme will largely consist of eight special Symposia and contributions (papers or posters) will be selected particularly within those topics. Contributions on other subjects will be considered at the discretion of the selection committee. There will be a Colloquium for Curators and a session on the European Invertebrate Survey, as well as the General Assembly of *Unitas Malacologica*. A full social programme including excursions is planned for participants and their partners.

The Symposia will be as follows: History of Malacology [to be held jointly with the Society for the History of Natural History in its jubilee year]; C.M. Yonge Commemorative: Bivalvia; Higher Classification and Phylogeny of the Prosobranchia; Applied Malacology; Cold-water Mollusca: Arctic, Antarctic and Deep-Sea; Introduced Species; Evolutionary Biology of Opisthobranchia; and Molluscs as Threatened Species: Their Exploitation and Conservation.

VERNACULAR NAMES FOR NORTH AMERICAN MOLLUSKS. – A preliminary list of scientific and vernacular names of mollusks has been prepared by a committee from the Council of Systematic Malacologists (CSM), American Malacological Union (AMU). The list is intended to cover those species occurring on the American continent north of Mexico and/or generally within 200 miles of its margin (to 200 m), including coastal islands, but not the West Indies. Principles governing the selection of common names were developed by the Names of Invertebrates Committee of the American Fisheries Society (AFS). This committee's main goal is to achieve uniformity and avoid confusion in vernacular nomenclature of aquatic invertebrates.

In 1983, CSM adopted the AFS principles and elected to join that Society's effort to establish common names for aquatic invertebrates. CSM's list covers living terrestrial, freshwater, and marine mollusks that have been previously described and published, preferably in monographed systematic works. Common names have been provided for most, but not all, species. AFS intends to publish the mollusk list developed by AMU within the next five years, and to publish a revision every ten years. The AFS list as it is developed and published will also include crustaceans, other groups of aquatic invertebrates, and probably terrestrial mollusks to show AFS' appreciation of CSM's and AMU's cooperative efforts.

Any questions on this CSM project should be directed to the committee chairman, Dr. Donna D. Turgeon, Regulations Branch Chief, F/M12, National Marine Fisheries Service, Page Building II, 3300 Whitehaven Street N.W., Washington, D.C. 20235, U.S.A. [phone 202-634-7432].

SIXTH CONGRESS OF THE SOCIÉTÉ FRANÇAISE DE MALACOLOGIE. – From 4-8 November 1985 the Société Française de Malacologie will hold its 6th Congress, at the Station Marine de Wimereux, Pas-de-Calais, France. The congress will include a symposium on "Ecotoxicologie et pollution des mollusques continentaux et marins". Further information can be obtained from Mr. J.M. Dewarumez, Station Marine, B.P. 41, 62930 Wimereux, France.

COURSE IN "BIOLOGY OF MOLLUSKS". – A field-oriented course in "Biology of Mollusks" will be taught by J.B. Burch at The University of Michigan Biological Station on Douglas Lake, Michigan, during the summer (late June to mid August) 1986. For further information, write to Director, University of Michigan Biological Station, The University of Michigan, Ann Arbor, Michigan 48109, U.S.A.

NEW JOURNAL IN MALACOLOGY. – The Chinese Society of Malacology of the People's Republic of China has distributed issue No. 1 of its new publication, *Transactions of the Chinese Society of Malacology*. This first number contains 228 pages plus cover pages, frontispiece, preface and table of contents, and includes 22 articles and an additional 20 abstracts. The articles are in Chinese, with English abstracts.

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REDACTIE: Dr. A. C. van Bruggen en Dr. E. Gittenberger.
Redactie-adres: Rijksmuseum van Natuurlijke Historie, Raamsteeg 2, Postbus 9517, 2300 RA Leiden.
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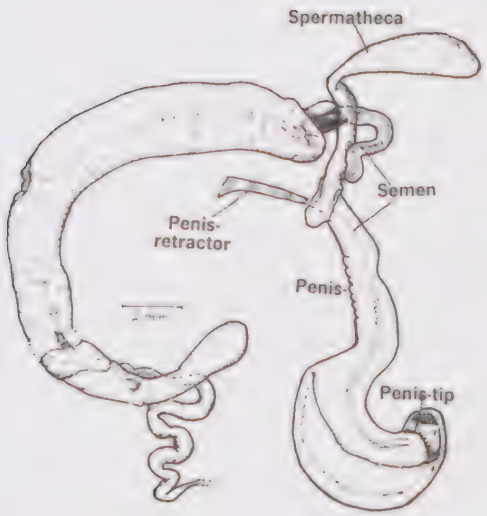

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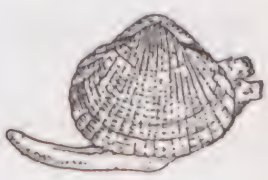

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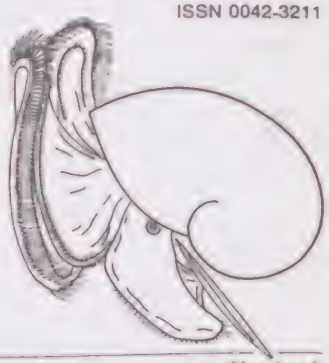

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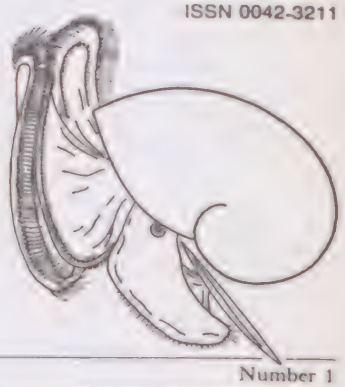

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Joint meeting with
The American Malacological Union

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MALACOLOGICAL ARTICLES IN SOME CURRENT BIOLOGICAL AND PALEONTOLOGICAL SERIAL PUBLICATIONS

In the last volume (Vol. 17) of *Malacological Review*, we initiated a new bibliographic feature, namely, the listing of all malacological articles that have appeared in several biological and paleontological serial publications. In Vol. 17 we included in our coverage the following publication series: *Proceedings of the Biological Society of Washington; Occasional Papers of the Museum of Zoology, The University of Michigan; Miscellaneous Publications of the Museum of Zoology, The University of Michigan;* Michigan Handbook Series, Museum of Zoology, The University of Michigan; Circular Series, Museum of Zoology, The University of Michigan; *Contributions in Science, Natural History Museum of Los Angeles County, California; Smithsonian Contributions to Zoology.*

Additions to two of the above serial publications, the *Proceedings of the Biological Society of Washington* and *Contributions in Science, Natural History Museum of Los Angeles County, California*, are listed below.

Proceedings of the Biological Society of Washington
Washington, D.C., U.S.A.

1980, Vol. 93, pp. 395-404. H. Lee Fairbanks and Richard L. Reeder. Two new species of *Sonorella* (Gastropoda: Pulmonata: Helminthoglyptidae) from the Pinaleno Mountains, Arizona.

1983, Vol. 96, pp. 250-252. Richard E. Petit. A new species of *Cancellaria* (Mollusca: Cancellariidae) from the northern Gulf of Mexico.

1983, Vol. 96, pp. 349-354. Richard S. Houbrick. A new *Strombina* species (Gastropoda: Prosobranchia) from the tropical western Atlantic.

1983, Vol. 96, pp. 355-364. James F. Quinn, Jr. *Carenzia*, a new genus of Seguenziacea (Gastropoda: Prosobranchia) with the description of a new species.

1983, Vol. 96, pp. 365-369. Ronald B. Toll. The lycoteuthid genus *Oregoniateuthis* Voss, 1956, a synonym of *Lycoteuthis* Pfeiffer, 1900 (Cephalopoda: Teuthoidea).

1983, Vol. 96, pp. 725-757. James F. Quinn, Jr. A revision of the Seguenziacea Verrill, 1884 (Gastropoda: Prosobranchia). I. Summary and evaluation of the superfamily.

1984, Vol. 97, pp. 86-89. Fred G. Thompson and Kurt Auffenberg. *Hypselostoma latispira*, a new pupillid land snail from the Philippine Islands.

1984, Vol. 97, pp. 179-185. H. Lee Fairbanks. A new species of *Oreohelix* (Gastropoda: Pulmonata: Oreohelicidae) from the Seven Devils Mountains, Idaho.

1984, Vol. 97, pp. 245-250. Barry Roth and Carl C. Christensen. A new *Gastrocopta* (Mollusca: Pulmonata: Pupillidae) from Baja California Sur, Mexico.

1984, Vol. 97, pp. 420-424. Richard S. Houbrick. A new "*Metula*" species from the Indo-West Pacific (Prosobranchia: Buccinidae).

Contributions in Science, Natural History Museum of Los Angeles County, California
Los Angeles, California, U.S.A.

1978, No. 299, 24 pp., 29 figs. Takeo Susuki and Carol J. Stadum. A Neogene section, northeastern San Clemente Island, California.

1979, No. 304, 8 pp., 6 figs. Louella R. Saul. A hollow spined *Anapachydiscus peninsularis* with possible Mosasaur bite impressions.

1982, No. 342, 20 pp., 56 figs. James H. McLean and Hector Andrade V. Large Archibenthal gastropods of Central Chile: collections from an expedition of the R/V Anton Bruun and the Chilean shrimp fishery.

1984, No. 350, 76 pp., 19 figs. Richard L. Squires. Megapaleontology of the Eocene Llajas Formation, Simi Valley, California.

1984, No. 351, 42 pp., 180 figs. Ellen J. Moore. Molluscan paleontology and biostratigraphy of the Lower Miocene upper part of the Lincoln Creek Formation in southwestern Washington.

It is our intention with each volume of *Malacological Review* to add to the list of serial publications covered. With the current issue, we are listing all malacological articles that have appeared in *American Museum Novitates* and *Palaeontographica Americana.*

American Museum Novitates
New York, New York, U.S.A.

1921, No. 28, 15 pp. Marjorie O'Connell. New species of ammonite opercula from the Mesozoic rocks of Cuba.
1930, No. 437, 4 pp. Chi Ping. Two new Cretaceous freshwater gastropods from Mongolia.
1931, No. 512, 11 pp. Curt Teichert. On the systematic position of the genus *Discosorus* Hall and related genera.
1934, No. 705, 16 pp. J. Bequaert and W.J. Clench. Studies of African land and freshwater mollusks. 3. West African Achatinae related to *Achatina balteata* Reeve.
1934, No. 746, 18 pp. H.N. Coryell and Eleanor S. Salmon. A molluscan faunule from the Pierre Formation in eastern Montana.
1934, No. 763, 26 pp. Ilse Rensch. Studies on *Papuina* and *Dendrotrochus*, pulmonate mollusks from the Solomon Islands.
1935, No. 764, 15 pp. Carlotta Joaquina Maury. New genera and new species of fossil terrestrial Mollusca from Brazil.
1937, No. 964, 13 pp. H.E. Vokes. Eocene Mollusca from the Subathu group (Lutetian), Simla Hills State, India.
1938, No. 988, 28 pp. H.E. Vokes. Upper Miocene Mollusca from Springvale, Trinidad, British West Indies.
1941, No. 1129, 21 pp. William J. Clench. The land Mollusca of the Solomon Islands (Succineidae, Bulimulidae, and Partulidae).
1941, No. 1145, 13 pp. H.E. Vokes. Contributions to the paleontology of the Lebanon Mountains, Republic of Lebanon. Part I. A Cenomanian pelecypod fauna from Hajula.
1942, No. 1182, 24 pp. Otto Haas. Some Upper Cretaceous ammonites from Angola.
1942, No. 1183, 8 pp. H.E. Vokes. Contributions to the paleontology of the Lebanon Mountains, Republic of Lebanon. Part II. Notes on *"Cardium" biseriatum* Conrad.
1943, No. 1222, 19 pp. Otto Haas. Some abnormally coiled ammonites from the Upper Cretaceous of Angola.
1943, No. 1223, 3 pp. Otto Haas. An Upper Albian ammonite from Mount Taylor Country [sic], New Mexico.
1945, No. 1286, 4 pp. Otto Haas. A recently acquired Albian ammonite from Angola.
1946, No. 1307, 9 pp. Otto Haas. Annotated faunal list of the Glen Dean Formation of Crane, Indiana.
1946, No. 1314, 8 pp. Henry Dodge. Notes on *Strombus dentatus* and the *Strombus urceus* complex.
1947, No. 1366, 4 pp. William Marcus Ingram. Additions to the knowledge of the Cypraeidae based on the collections of the American Museum of Natural History.
1948, No. 1374, 4 pp. William J. Clench and Ruth D. Turner. A new *Thais* from Angola and notes on *Thais haemastoma* Linne.
1951, No. 1481, 5 pp. Teng-Chien Yen. Some Lower Cretaceous pelecypods from Pryor, Montana.
1951, No. 1490, 21 pp. Otto Haas. Supplementary notes on the ammonoid genus *Dunveganoceras*.
1952, No. 1560, 3 pp. H.E. Vokes. Notes on the pelecypod genus *Platopsis* Whitfield.
1952, No. 1561, 17 pp. Otto Haas. Some Albian desmoceratid and lytoceratid ammonoidea from Angola.
1955, No. 1713, 15 pp. L.J. Chubb. A revision of Whitfield's type specimens of the rudist mollusks from the Cretaceous of Jamaica, British West Indies.
1956, No. 1761, 17 pp. Henry E. Crampton. New species of land snails of the genus *Partula* from Raiatea, Society Islands.
1956, No. 1787, 7 pp. William K. Emerson. A new scaphopod mollusk, *Dentalium (Tesseracme) hancocki*, from the eastern Pacific.
1956, No. 1794, 3 pp. William J. Clench. A new *Cerion* from Bimini, Bahamas (Mollusca).
1956, No. 1796, 21 pp. Eveline and Ernst Marcus. On two sacoglossan slugs from Brazil.
1956, No. 1799, 13 pp. Norman D. Newell. Primitive desmodont pelecypods of the Australian Permian.
1956, No. 1806, 48 pp. Ernst Mayr and Carmela Berritto Rosen. Geographic variation and hybridization in populations of Bahama snails (*Cerion*).
1957, No. 1825, 57 pp. William K. Emerson and Elton L. Puffer. Recent mollusks of the 1940 "E.W. Scripps" cruise to the Gulf of California.
1957, No. 1857, 16 pp. Norman D. Newell. Notes on certain primitive heterodont pelecypods.
1957, No. 1859, 9 pp. Leo George Hertlein and William K. Emerson. Additional notes on the invertebrate fauna of Clipperton Island.

1957, No. 1863, 6 pp. William J. Clench. New land Mollusca from the Admiralty and Bismarck islands.
1958, No. 1878, 6 pp. Norman D. Newell. A note on Permian crassatellid pelecypods.
1958, No. 1899, 14 pp. Morris K. Jacobson. Results of the Puritan-American Museum of Natural History expedition to western Mexico 3. The terrestrial mollusks.
1958, No. 1906, 82 pp. Ernst Marcus. On western Atlantic opisthobranchiate gastropods.
1958, No. 1909, 11 pp. William K. Emerson and Warren O. Addicott. Pleistocene invertebrates from Punta Baja, Baja California, Mexico.
1959, No. 1925, 33 pp. Warren O. Addicott and William K. Emerson. Late Pleistocene invertebrates from Punta Cabras, Baja California, Mexico.
1959, No. 1940, 15 pp. Leo G. Hertlein and William K. Emerson. Results of the Puritan-American Museum of Natural History expedition to western Mexico 5. Pliocene and Pleistocene megafossils from the Tres Marias Islands.
1959, No. 1974, 8 pp. William K. Emerson. the Gastropod genus *Pterorytis*.
1960, No. 1995, 6 pp. William K. Emerson. Results of the Puritan-American Museum of Natural History expedition to western Mexico 11. Pleistocene invertebrates from Ceralvo Island.
1960, No. 2002, 7 pp. William K. Emerson. Pleistocene invertebrates from near Punta San Jose, Baja California, Mexico.
1960, No. 2004, 8 pp. William K. Emerson and Leo George Hertlein. Pliocene and Pleistocene invertebrates from Punta Rosalia, Baja California, Mexico.
1960, No. 2005, 62 pp. Otto Haas. Lower Cretaceous ammonites from Colombia, South America.
1960, No. 2009, 15 pp. William K. Emerson. Remarks on some eastern Pacific muricid gastropods.
1960, No. 2013, 9 pp. William K. Emerson. Results of the Puritan-American Museum of Natural History expedition to western Mexico. 12. Shell middens of San Jose Island.
1962, No. 2108, 8 pp. William K. Emerson and Anthony D'Attilio. Remarks on *Triton ranzanii* Bianconi (Mollusca, Gastropoda).
1962, No. 2112, 44 pp. William K. Emerson and William E. Old, Jr. Results of the Puritan-American Museum of Natural History expedition to western Mexico 16. The Recent mollusks: Gastropoda, Conidae.
1962, No. 2121, 4 pp. Norman D. Newell and Kenneth W. Ciriacks. A new bivalve from the Permian of the western United States.
1963, No. 2136, 32 pp. William K. Emerson and William E. Old, Jr. Results of the Puritan-American Museum of Natural History expedition to western Mexico 17. The Recent mollusks: Gastropoda, Cypraeacea.
1963, No. 2137, 13 pp. William K. Emerson and William E. Old, Jr. A new subgenus and species of *Cymatium* (Mollusca, Gastropoda).
1963, No. 2149, 9 pp. William K. Emerson and Anthony D'Attilio. A new species of *Latiaxis* from the western Atlantic (Mollusca, Gastropoda).
1963, No. 2151, 19 pp. Otto Haas. *Paracanthoceras wyomingense* (Reagan) from the western interior of the United States and from Alberta (Ammonoidea).
1963, No. 2153, 38 pp. William K. Emerson and Anthony D'Attilio. Results of the Puritan-American Museum of Natural History expedition to western Mexico 19. The Recent mollusks: Gastropoda, Strombacea, Tonnacea, and Cymatiacea.
1964, No. 2165, 16 pp. Roger L. Batten. Some Permian gastropods from eastern Arizona.
1964, No. 2202, 23 pp. William K. Emerson. Results of the Puritan-American Museum of Natural History expedition to western Mexico 20. The Recent mollusks: Gastropoda: Harpidae, Vasidae, and Volutidae.
1965, No. 2206, 25 pp. Norman D. Newell. Classification of the Bivalvia.
1965, No. 2215, 11 pp. Kenneth J. Boss. A new mollusk (Bivalvia, Erycinidae) commensal on the stomatopod crustacean *Lysiosquilla*.
1965, No. 2218, 12 pp. William K. Emerson. The eastern Pacific species of *Niso* (Mollusca: Gastropoda).
1966, No. 2242, 7 pp. Harold B. Rollins. Morphological observations on the bellerophont *Ptomatis patulus* (Hall) (Gastropoda, Bellerophontacea).
1966, No. 2263, 13 pp. Stephen Jay Gould. Notes on shell morphology and classification of the Siliquariidae (Gastropoda). The protoconch and slit of *Siliquaria squamata* (Blainville).
1968, No. 2328, 52 pp. Donald W. Boyd and Norman D. Newell. Hinge grades in the evolution of crassatellacean bivalves as revealed by Permian genera.
1969, No. 2368, 33 pp. Eveline Marcus and Ernst Marcus. Opisthobranchian and lamellarian gastropods collected by the "Vema".
1970, No. 2414, 29 pp. James Nybakken. Radular anatomy and systematics of the West American Conidae (Mollusca, Gastropoda).
1972, No. 2501, 34 pp. Roger L. Batten. The ultrastructure of five common Pennsylvanian pleurotomarian gastropod species of the eastern United States.
1974, No. 2533, 19 pp. Bruce Runnegar and Norman D. Newell. *Edmondia* and the Edmondiacea shallow burrowing Paleozoic pelecypods.

1975, No. 2567, 29 pp. Roger L. Batten. The Scissurellidae – are they neotenously derived fissurellids? (Archaeogastropoda).
1975, No. 2579, 35 pp. Harold B. Rollins. Gastropods from the Lower Mississippian Wassonville limestone in southeastern Iowa.
1979, No. 2685, 26 pp. Roger L. Batten. Gastropods from Perak, Malaysia part 2. The trochids, patellids, and neritids.
1979, No. 2686, 22 pp. Donald W. Boyd and Norman D. Newell. Permian pelecypods from Tunisia.
1984, No. 2776, 13 pp. Roger L. Batten. Shell structure of the Galapagos rift limpet *Neomphalus fretterae* McLean, 1981, with notes on muscle scars and insertions.

Palaeontographica Americana
Ithaca, New York, U.S.A.

1917, Vol. 1, pp. 1-104. Pearl G. Sheldon. Atlantic Slope arcas.
1920, Vol. 1, pp. 105-118. Gilbert D. Harris. The genera *Lutetia* and *Alveinus* especially as developed in America.
1922, Vol. 1, pp. 119-162. G.D. Harris and Floyd Hodson. The rudistids of Jamaica.
1922, Vol. 1, pp. 162-206. Carlotta J. Maury. The Recent arcas of the Panamic province.
1929, Vol. 1, pp. 207-519. Katherine Van Winkle Palmer. The Veneridae of Eastern America, Cenozoic and Recent.
1937, Vol. 2, pp. 23-145. Gilbert D. Harris. Turrid illustrations, mainly Claibornian.
1938, Vol. 2, pp. 146-163. Katherine Van Winkle Palmer. Neocene Spondyli from the southern United States and tropical America.
1938, Vol. 2, pp. 164-247. Rousseau H. Flower. Devonian brevicones of New York and adjacent areas.
1938, Vol. 2, pp. 248-561. Rousseau H. Flower. Study of the Pseudorthoceratidae.
1940, Vol. 2, pp. 561-571. Burnett Smith. Notes on the giant fasciolarias.
1941, Vol. 3, pp. 1-56. Rousseau H. Flower. Notes on structure and phylogeny of eurysiphonate cephalopods.
1943, Vol. 3, pp. 91-98. Burnett Smith. Two abnormal *Busycon* shells.
1944, Vol. 3, pp. 165-172. Burnett Smith. Two spine rows in a Florida *Busycon contrarium*.
1944, Vol. 3, pp. 225-272. Burnett Smith. Observations on gastropod protoconchs pts. I and II.
1946, Vol. 3, pp. 287-304. Burnett Smith. Observations on gastropod protoconchs III. Some protoconchs in *Busycon, Fusinus, Heilprinia, Hesperisternia* and *Urosalpinx*.
1948, Vol. 3, pp. 305-320. Burnett Smith. Two marine Quaternary locations.
1950, Vol. 3, pp. 361-396. Rousseau H. Flower. *Stereoceras* and the Brevicoceratidae.
1953, Vol. 3, pp. 397-508. P. Verastegui. The pelecypod genus *Venericardia* in the Paleocene and Eocene of western North America.
1956, Vol. 4, pp. 1-31. L.J. Chubb. Some rarer rudists from Jamaica.
1956, Vol. 4, pp. 32-50. L.J. Chubb. *Thyrostylon*, a new rudist genus from the Upper Cretaceous of Guatemala, the Antilles, and Persia, with a discussion of the functions of rudist ossicles and pillars.
1958, Vol. 4, pp. 39-118. Solomon C. Hollister. A review of the genus *Busycon* and its allies.
1962, Vol. 4, pp. 157-205. John Pojeta, Jr. The pelecypod genus *Byssonychia* as it occurs in the Cincinnatian at Cincinnati, Ohio.
1964, Vol. 4, pp. 354-495. Angelo Heilprin. Exploration on the west coast of Florida (reprint).
1965, Vol. 5, pp. 1-62. S.O. Bird. Upper Tertiary Arcacea of the mid-Atlantic coastal plain.
1965, Vol. 5, pp. 63-127. Egbert G. Driscoll. Dimyarian pelecypods of the Mississippian Marshall sandstone of Michigan.
1966, Vol. 5, pp. 128-241. John Pojeta, Jr. North American Ambonychiliidae (Pelecypoda).
1968, Vol. 6, pp. 51-85. William G. Heaslip. Cenozoic evolution of the alticostate venericards in Gulf and East coastal North America.
1970, Vol. 7, pp. 1-14. Peter Jung. *Torreites sanchezi* (Douville) from Jamaica.
1970, Vol. 7, pp. 14-24. Axel A. Olsson. The cancellariid radula and its interpretation.
1971, Vol. 7, pp. 157-257. L.J. Chubb. Rudists of Jamaica.
1974, Vol. 8, pp. 1-72. Peter Jung. A revision of the family Seraphsidae (Gastropoda: Strombacea).
1976, Vol. 8, pp. 214-331. Sara Bretsky. Evolution and classification of Cenozoic North American and European Lucinidae (Mollusca: Bivalvia).
1980, Vol. 9, pp. 1-93. R.L. Hall and G.E.G. Westermann. Lower Bajocian (Jurassic) cephalopod faunas from western Canada, and proposed assemblage zones for the Lower Bajocian of North America.

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MALACOLOGICAL NEWSLETTERS

During the past two years, *Malacological Review* has received the malacological society newsletters listed below. Due to lack of space, the contents of these newsletters is not presented below, but will be given in Vol. 19.

A.M.U., Inc. Newsletter
c/o Paula M. Mikkelsen
Harbor Branch Foundation, Inc.
R.R. 1, Box 196
Ft. Pierce, Florida 33450
U.S.A.

Arion
Bulletin de Contact de la Société Belge de Malacologie
Av. Mozart, 52
B-1190 Bruxelles
Belgium

Australian Shell News
Newsletter of the Malacological Society of Australia
c/o Museum of Victoria
285 Russell Street
Melbourne, Victoria 3000
Australia

Donax Panamensis
Sociedad Panameña de Malacología
Apartado 6-593
El Dorado
Rep. de Panamá

Informativo S.B.M.
Sociedade Brasileira de Malacologia
c/o Departamento de Zoologia
Instituto de Biociencias U.S.P.
C.P. 20.520
CEP 01000 São Paulo, SP
Brazil

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A Malacological Newsletter
Published by the Israel Malacological Society and
the Municipal Malacological Museum, Nahariya
P. O. Box 6012
31060 Haifa
Israel

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PUBLICATIONS*

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Books

BOYLE, P.R. (Ed.) 1983. *Cephalopod life cycles. Volume I. Species accounts.* Academic Press, New York. 475 pp.

CVANCARA, Alan M. 1983. *Aquatic mollusks of North Dakota.* Report of Investigation No. 78, North Dakota Geological Survey. i-v, 1-141 pp. US$5.00.

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